Scavenging Ecology in the Australian Alps

The bottom-side to the circle of life

Chris Fust
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A thesis submitted to fulfil requirements for the degree of Master of Philosophy in the School of Life and Environmental Sciences

School of Life and Environmental Sciences
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Figure 1: A view of Mount Kosciuszko (far left) from Charlotte Pass in Kosciuszko National Park. This is the highest elevation in Australia at 2,228 metres above sea level and one of the few places on the continent that receives annual snowfall. The surrounding alpine and subalpine of Kosciuszko National Park are home to many unique species having one of the highest rates of endemism of any temperate montane environment.

Declaration

This is to certify that to the best of my knowledge, the content of this thesis is my own work. This thesis has not been submitted for any degree or other purposes.

I certify that the intellectual content of this thesis is the product of my own work and that all the assistance received in preparing this thesis and sources have been acknowledged.

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December 2021

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Foreword

It was a big shock when the research I worked on 12,000 kilometres away was presented to me in a lecture by none-other than Dr Thomas Newsome in his terrestrial ecology course. I had spent the better half of a decade working as a research technician for an ecology project on cougars (*Puma concolor*) in the United Sates and now, literally on the other side of the planet, I was being lectured on the work I participated in. No way was this just a coincidence. Dr Newsome was presenting a slide on "The Landscape of Fear" and all those memories of the years I spent traipsing around the bush hauling road-kill deer (*Odocoileus hemionus*) around to bait cougars for science came flooding back. From that moment, I knew I wanted to work with Dr Newsome but hadn't the slightest clue as to what that would be. It was quite a shock again to hear Dr Newsome say that the project he had available required the exact specific skill set I possess: hauling around animal carcasses for science. Fate struck once again. I may not pride myself on this unique skill set, but at least I've had practice. Since that moment in his office, I've come to appreciate the place in which this research sits. Scavenging may not be a "pretty" concept to think about, but it is a keystone part of every ecosystem and there is a beauty in its process; recycling nutrients for the benefit of new life.

Acknowledgements

This has been a long and arduous yet rewarding project producing close to a million images and thirty-thousand sampled insects over the course of almost four-hundred monitoring days. With that, I want to thank the people behind the vision of this project, Dr Thomas Newsome, Dr Philip Barton, and Emma Spencer for creating a base of scavenging research that I could build upon. Without their foundational research, guidance, and funding my research project would be lost. They have built an amazing research lab one which I think will continue to grow and flourish.

I want to thank my supervisors Dr Thomas Newsome, Dr Philip Barton, and Dr Mathew Crowther for their support above and beyond the call of duty in constructively critiquing my ideas as a scientist and all the work they've put in reviewing my manuscript. I've always struggled with thinking my ideas weren't worthy of the scientific community, yet here I have produced what equates to a short novel on a humble experiment. With their guidance I finally feel competent and confident enough to call myself a scientist.

Thank you, James Vandersteen, for the hard work you've put into this joint project. I really can't thank you enough for all the time and energy you put into fieldwork. It's been almost three years of research on our projects, and I finally think we can see them as huge accomplishments in our lives.

I wish you the best as you continue your path of science. P.S.: I wouldn't want to haul carrion around with anyone else.

Thank you, Stef Bonat and Rhys Cairncross, for your critical support in the field and in the lab. You two have always had amazing positive attitudes though the most tedious moments. Sharing those moments of research struggles helped turn some of them into great positive memories.

To the Global Ecology Lab, thank you for all your support in our meetings and giving constructive criticism. It has been invaluable to have your ideas and use them in crafting this science project. I can't wait to see the discoveries you all will find.

Thank you, Ted Rowley, and Jo Oddie, for your support and your accommodation. James, Stef, and I were just lost students, aimlessly wandering around the bush trying to put connections together with scotch-tape and glue. If it weren't for your expertise and generosity—from networking to mechanics—we'd still be trying to contact suppliers and living out of our tents. Our lab is grateful for your kindness.

Thank you, Mel Schroder, Rob Gibbs, Andrew Miller, and the rest of the National Parks and Wildlife Service members who supported this project's operation in Kosciuszko NP in the form of access and accommodation. Thank you for letting me roam around the park and really get to love that land.

Thank you, Matt Smith, Ben Viola, and Nicholas Whyte, for volunteering your time in such a wacky science project. Y'all never blinked twice when James recruited you to haul around carrion and I can't thank you enough. Your help was critical.

To Tianna Grant, I want to thank you most of all for your love and support while I tromped around the bush. Thank you not only for help in the field but for supporting me though this difficult journey. Thank you for believing in me when this project had its difficulties. Thank you for being patient with me when I was away with field work. Thank you for exploring Kosciuszko with me and making some of the best memories of the park. This has been a long, hard project and I'm so glad to finally tell you it's completed.

Photographic Credits

Chris Fust
Images of insects, landscapes, diagrams, and maps

James Vandersteen
Remote camera images of wildlife at carrion at open sites

Stef Bonat
Graphic of Scavengers in Kosciuszko National Park in introduction

Dr Thomas Newsome
Diagram of scavenging food web and Miscellaneous in introduction

Abstract

Scavenging is the consumption of carrion by living organisms (Olea et al., 2019a). Although often overlooked and colloquially thought of as repugnant, it is common in all ecosystems (Wilson and Wolkovich, 2011). Indeed, in terrestrial food webs detritus consumed from animal remains can represent a disproportionately larger and more abundant resource than that consumed from predation, yet its use by living organisms is not as well understood (Barton et al., 2013; Devault et al., 2003; Olea et al., 2019a). Carrion can support an immense diversity of species whose colonisation and utilisation influence its decomposition (Barton et al., 2013; Mateo-Tomás et al., 2015; Selva et al., 2005). The assemblage of scavengers that act on the carcass are ecologically important in maintaining this ecosystem service (Huijbers et al., 2015; Lawton and Brown, 1994) and are part of the necrobiome (Benbow et al., 2019). Scavengers can be classified into distinct scavenger guilds comprised of vertebrates, invertebrates, and microorganisms whose collaborative roles operate most efficiently when their community structure is diverse and left intact (Barton et al., 2013; Bastolla et al., 2009; Rohr et al., 2014; Wilson and Wolkovich, 2011).

The goal of this thesis is to quantify how different scavenger guilds can influence decay rates (carcass persistence), and how invertebrate scavengers respond to the absence of competition from vertebrate scavengers (Barton et al., 2013; Devault et al., 2003; Putman, 1978). Individually, the functional roles vertebrate and invertebrate scavengers are known (Barton and Bump, 2019), but there is limited understanding about how their interactions with each other influence decay rates (Benbow et al., 2015b). Understanding the factors that influence carcass persistence rates is important as it influences how energy flows throughout food webs (Beasley et al., 2015; Ogada et al., 2012; Putman, 1978). Changes in the composition of vertebrate and invertebrate scavenger communities around carcasses may prolong carrion persistence (Beasley et al., 2012; Payne, 1965) possibly altering the localised effects of nutrient flow and increase the chance of carcass borne disease spread (Beasley et al., 2015; Markandya et al., 2008; Olea et al., 2019a).

Understanding how scavenger guilds interact and their effects on carcass persistence is particularly important in the Snowy Mountains region of south-eastern Australia where land managers cull both large herbivores (predominantly kangaroos and feral deer) and facultative vertebrate scavengers possibly creating and influx of carrion and altering the functionality of the vertebrate scavenger guild (Independent Scientific Committee (N.S.W.), 2003; Mules, 2005; New South Wales et al., 2006). Herbivore culls present as stochastic temporary acute surges of biomass that are highly sought-after by scavengers. However, large deposits of animal biomass may have negative impacts on the local environment and health of wildlife and humans through unregulated nutrient release and disease spread (O'Bryan et al., 2018), or even by increasing scavenging opportunities for invasive

species (Spencer et al., 2021). Therefore, it is important to understand the natural processes by which it is broken down, dispersed, and reabsorbed into the surrounding ecosystem through scavenging (Figure 2).

Using exclusion cages that limit vertebrate and invertebrate scavengers' access to carrion, this study was able assess each guild's individual contributions to carcass persistence by removing inter-guild competition. In contrast to similar systems, utilisation of carcasses by vertebrates did little to influence decay rates. This was pronounced in autumn and winter when carcasses persisted the longest despite elevated vertebrate activity and reduced competition from insects and microbes. This shifts the function of carrion removal towards insects as vertebrates contribute little to decomposition leading to a reduction of resiliency of this process. Additionally, due to the highly variable climate in the Snowy Mountains region in Australia (Australian Alps)—with winter temperatures down to -4°C and summer temperatures reaching 19°C (Bureau of Meteorology, 2020)—decay rates are further impacted as low temperatures suppress insect and microbial activity. The seasonal capacities of the vertebrate and insect scavengers of this system display a reduction in this ecosystem's ability to recycle carrion during cold seasons.

The efficiency and manner of which vertebrates and insects scavenge and consume carcasses is ecologically important and may be used as an indicator of how intact ecosystems are (Newsome et al., 2021) as well as providing feedback to natural resource managers whether there is a need to manage carcass loads. To date, there are few studies globally that have simultaneously examined both insect and vertebrate scavenging guilds around carrion. This study aims to fill this knowledge gap and explore how these scavenging guilds interact, and whether the absence of one or both guilds have the capacity to influence carcass persistence.

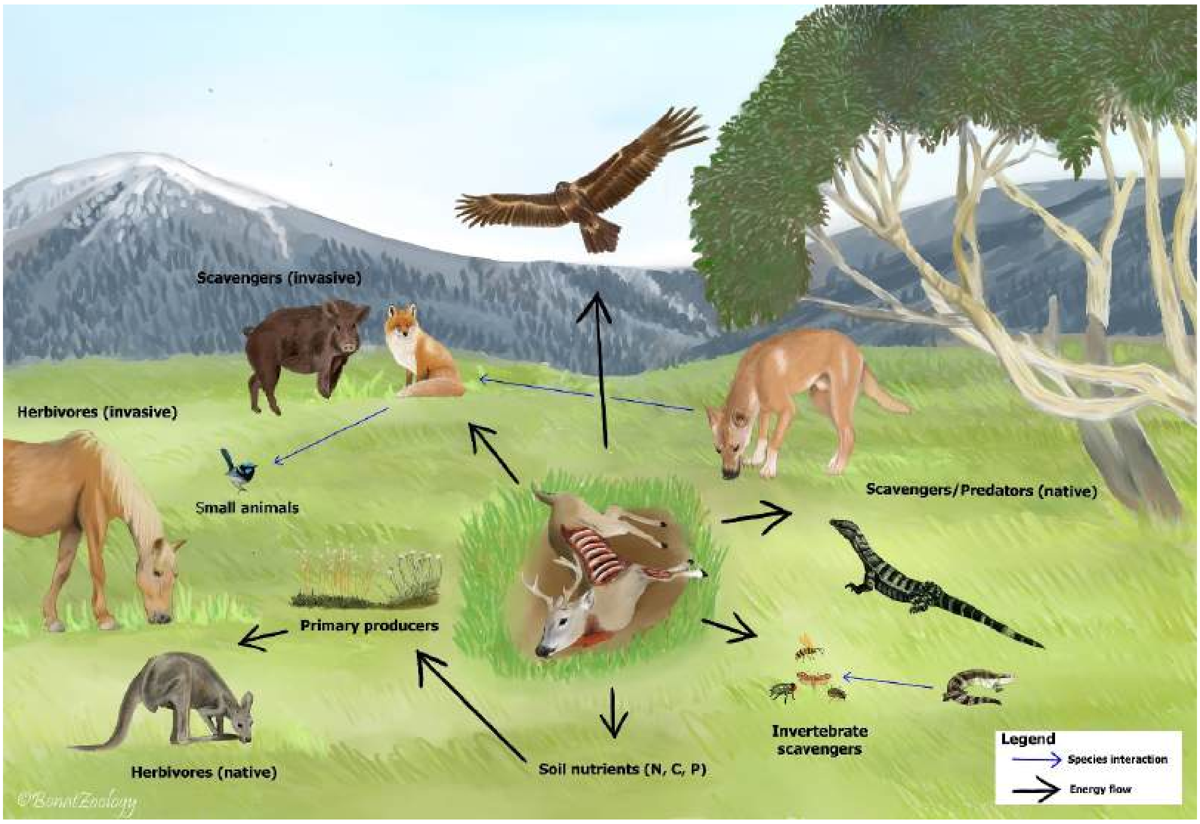

Figure 2: The necrobiome of the Snowy Mountains region of south-eastern Australia as depicted by Stef Bonat (@BonatZoology). Carcasses of mammals are fed upon by microbes, insects (e.g. ants, beetles, flies, and wasps), and vertebrates (e.g. corvids, birds of prey, possums, dingoes, cats, pigs, and foxes). Rates of scavenging can influence other ecosystem processes linked to decomposition such as soil properties, plant growth or use of the carcass site by herbivores and pollinators. Insects are more active in warmer months and could potentially outcompete vertebrates at carrion resources during that time. Vertebrates could be more active at carcasses in colder months but may not have the functional capacity to remove carcass biomass in the absence of insects. This thesis will explore these dynamics.

References

Barton, P.S., Bump, J.K., 2019. Carrion Decomposition, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 101–124. https://doi.org/10.1007/978-3-030-16501-7_5

Barton, P.S., Cunningham, S.A., Lindenmayer, D.B., Manning, A.D., 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia 171, 761–772. https://doi.org/10.1007/s00442-012-2460-3

Bastolla, U., Fortuna, M.A., Pascual-García, A., Ferrera, A., Luque, B., Bascompte, J., 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature 458, 1018–1020. https://doi.org/10.1038/nature07950

Beasley, J.C., Olson, Z.H., DeVault, T.L., 2015. Ecological role of vertebrate scavengers. CRC Press. https://doi.org/10.1201/b18819

Beasley, J.C., Olson, Z.H., Devault, T.L., 2012. Carrion cycling in food webs: Comparisons among terrestrial and marine ecosystems. Oikos 121, 1021–1026. https://doi.org/10.1111/j.1600-0706.2012.20353.x

Benbow, M., Barton, P., Ulyshen, M., Beasley, J., DeVault, T., Strickland, M., Tomberlin, J., Jordan, H., Pechal, J., 2019. Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. Ecological Monographs 89. https://doi.org/10.1002/ecm.1331

Benbow, M.E., Tomberlin, J.K., Tarone, A.M. (Eds.), 2015. Carrion Ecology, Evolution, and Their Applications. CRC Press, Boca Raton. https://doi.org/10.1201/b18819

Bureau of Meteorology, 2020. Summary statistics MOUNT KOSCIUSKO (HOTEL KOSCIUSKO) [WWW Document]. URL http://www.bom.gov.au/climate/averages/tables/cw_071012.shtml (accessed 11.4.20).

Devault, T.L., Rhodes, O.E., Shivik, J.A., Devault, T.L., Rhodes, O.E., Shivik, J.A., 2003. Scavenging by Vertebrates : Behavioral , Ecological , and Evolutionary Perspectives on an Important Energy Transfer Pathway in Terrestrial Ecosystems Published by : Wiley on behalf of Nordic Society Oikos Stable URL : http://www.jstor. Oikos 102, 225–234.

Huijbers, C.M., Schlacher, T.A., Schoeman, D.S., Olds, A.D., Weston, M.A., Connolly, R.M., 2015. Limited functional redundancy in vertebrate scavenger guilds fails to compensate for the loss of raptors from urbanized sandy beaches. Diversity and Distributions 21, 55–63. https://doi.org/10.1111/ddi.12282

Independent Scientific Committee (N.S.W.), 2003. An assessment of the values of Kosciuszko National Park : interim report. National Parks and Wildlife Service, Queanbeyan NSW.

Lawton, J.H., Brown, V.K., 1994. Redundancy in Ecosystems, in: Schulze, E.-D., Mooney, H.A. (Eds.), Biodiversity and Ecosystem Function, Praktische Zahnmedizin Odonto-Stomatologie Pratique Practical Dental Medicine. Springer, Berlin, Heidelberg, pp. 255–270. https://doi.org/10.1007/978-3-642-58001-7_12

Markandya, A., Taylor, T., Longo, A., Murty, M.N., Murty, S., Dhavala, K., 2008. Counting the cost of vulture decline—An appraisal of the human health and other benefits of vultures in India. Ecological Economics, Special Section: Biodiversity and Policy 67, 194–204. https://doi.org/10.1016/j.ecolecon.2008.04.020

Mateo-Tomás, P., Olea, P.P., Moleón, M., Vicente, J., Botella, F., Selva, N., Viñuela, J., Sánchez-Zapata, J.A., 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. Diversity and Distributions 21, 913–924. https://doi.org/10.1111/ddi.12330

Mules, T., 2005. Economic Impacts of National Park Tourism on Gateway Communities: The Case of Kosciuszko National Park. Tourism Economics 11, 247–259. https://doi.org/10.5367/0000000054183513

New South Wales, Department of Environment and Conservation, Parks and Wildlife Division, New South Wales, Department of Environment and Conservation, 2006. Kosciuszko National Park plan of management: 2006. Dept. of Environment and Conservation NSW, Sydney South, N.S.W.

Newsome, T.M., Barton, B., Buck, J.C., DeBruyn, J., Spencer, E., Ripple, W.J., Barton, P.S., 2021. Monitoring the dead as an ecosystem indicator. Ecology and Evolution 11, 5844–5856. https://doi.org/10.1002/ece3.7542

O'Bryan, C.J., Braczkowski, A.R., Beyer, H.L., Carter, N.H., Watson, J.E.M., McDonald-Madden, E., 2018. The contribution of predators and scavengers to human well-being. Nat Ecol Evol 2, 229–236. https://doi.org/10.1038/s41559-017-0421-2

Ogada, D.L., Torchin, M.E., Kinnaird, M.F., Ezenwa, V.O., 2012. Effects of Vulture Declines on Facultative Scavengers and Potential Implications for Mammalian Disease Transmission: *Vulture Declines, Facultative Scavengers, and Disease Transmission*. Conservation Biology 26, 453–460. https://doi.org/10.1111/j.1523-1739.2012.01827.x

Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), 2019. Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-030-16501-7

Payne, J.A., 1965. A Summer Carrion Study of the Baby Pig Sus Scrofa Linnaeus. Ecology 46, 592–602. https://doi.org/10.2307/1934999

Putman, R.J., 1978. Flow of Energy and Organic Matter from a Carcase during Decomposition: Decomposition of Small Mammal Carrion in Temperate Systems. Oikos 31, 58–68. https://doi.org/10.2307/3543384

Rohr, R.P., Saavedra, S., Bascompte, J., 2014. On the structural stability of mutualistic systems. Science 345, 1253497–1253497. https://doi.org/10.1126/science.1253497

Selva, N., Jędrzejewska, B., Jedrzejewski, W., Wajrak, A., 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. Canadian Journal of Zoology 83, 1590–1601. https://doi.org/10.1139/z05-158

Spencer, E.E., Dickman, C.R., Greenville, A., Crowther, M.S., Kutt, A., Newsome, T.M., 2021. Carcasses attract invasive species and increase artificial nest predation in a desert environment. Global Ecology and Conservation 27, e01588. https://doi.org/10.1016/j.gecco.2021.e01588

Wilson, E.E., Wolkovich, E.M., 2011. Scavenging: How carnivores and carrion structure communities. Trends in Ecology and Evolution 26, 129–135. https://doi.org/10.1016/j.tree.2010.12.011

Introduction

Scavenging and the Australian Alps

Introduction: Scavenging and the Australian Alps

Figure 3: Example of necrophilous species within Kosciuszko National Park. Left, dingo (*Canis lupus dingo*). Right, necrophilous beetles (Devil's Coach Horse: *Creophilous erythrocephalus* and carrion beetle: *Ptomophila lacrymosa*)

Carrion and its Characteristics

Carrion is a highly sought-after resource but it is ephemeral and stochastic in nature (Moleón et al., 2019). Nonetheless, animals seek out carrion because there is less risk of injury compared to hunting live prey. Compared to plant biomass, animal biomass is much more nutrient dense and is delivered in a more easily accessible form for animals to process (Benbow et al., 2019; Carter et al., 2007). It can also be more common than live prey as more animals die due to other causes than predation (Carter et al., 2007). This combination of an easily accessible and nutrient rich resource is what makes it so sought-after but the difficulty in capitalising this free resource comes from 1) its stochastic placement in space and time, and 2) its fleeting availability as it decomposes (Moleón et al., 2019; Olea and Mateo-Tomas, 2009; Pereira et al., 2014; Wilmers and Getz, 2004; Wilmers and Post, 2006). For species that utilise carrion, this demands adaptation and specialisation and is why most vertebrate predators are facultative scavengers (predators that subsidise their diet with carrion) (Charabidze et al., 2021; Devault et al., 2003; Evans et al., 2020). Most scavenging vertebrates, aside from vultures, lack the ability to persist solely off carrion due to the energy constraints of locating viable carrion (Devault et al., 2003). Some scavenging insects, however, have a different metabolic pattern and have adapted a rapid community response to carrion allowing them to specialise and persist almost entirely from this resource (Evans et al., 2020). The competition between these scavenging guilds, in terms of utilising carcass resources, creates a redundancy and robustness to the ecosystem with respect to accelerating carcass biomass removal (Biggs et al., 2020).

Emergence of Scavenging Research

Scavenging is an emergent subject in ecology (Benbow et al., 2015b; Olea et al., 2019a), and monitoring of food web dynamics around carrion has recently been proposed as a tool to assess ecosystem function and integrity (Newsome et al., 2021). Scavenging ecology by its nature is a study of how energy flows through a community of organisms. The new-found interest in carrion ecology can be seen in the number of publications through time. A topic search of necrobiome ecology on the Web of Science database using the terms “scavenging ecology” (TS=(CARCASS) AND TS=(ECOLOGY)) OR (TS=(CARRION) AND TS=(ECOLOGY)) OR (TS=(SCAVENG*) AND TS=(ECOLOGY)) shows a recent increase in publications on the subject (Figure 4). The research to date has helped to characterise the roles of different scavenger guilds (Beasley et al., 2015; Crippen et al., 2015; Merritt and Jong, 2015), but few studies that have simultaneously assessed the roles of both vertebrates and invertebrates (Figure 5).

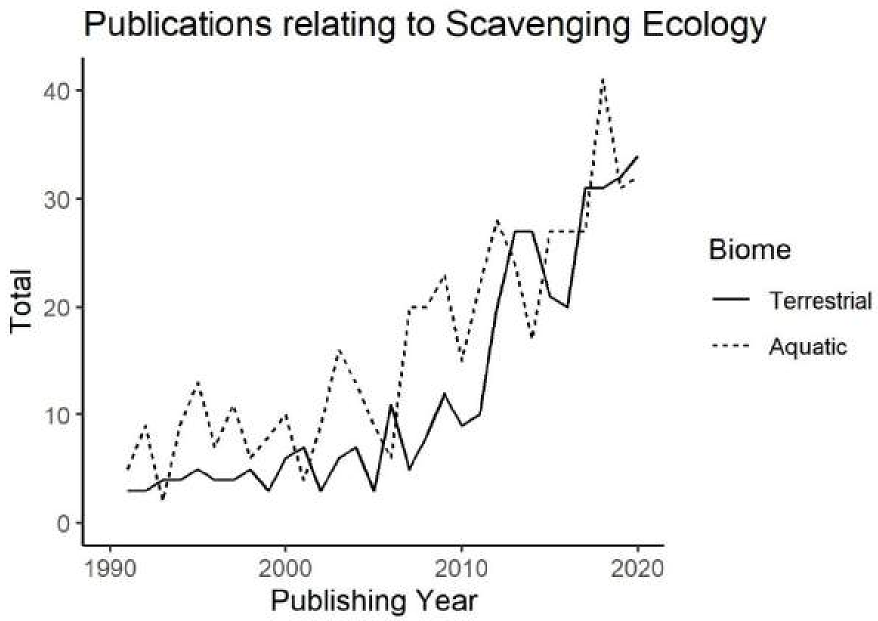

Figure 4: Scavenging ecology is a growing topic in ecological research that has seen a rapid increase of publications each year. A search on the Web of Science Database for the topic (TS) "SCAVENGING ECOLOGY" shows this increase. This search’s terms are (TS=(CARCASS) AND TS=(ECOLOGY)) OR (TS=(CARRION) AND TS=(ECOLOGY)) OR (TS=(SCAVENG*) AND TS=(ECOLOGY)) and limited between 1990-01-01 to 2021-01-01. Publications were then evaluated if their subject matter had scavenging is as a primary research topic and tagged such. Publications were also tagged with “terrestrial” or “aquatic” dependent on their context. This search yielded 1,723 relevant publications.

The lack of studies assessing the roles of both vertebrates and invertebrates represents a major knowledge gap (Barton et al., 2013). Vertebrate and insect scavengers interact on carcasses with a mixture of competitive and complimentary roles on carrion. Indeed, vertebrate scavengers add a component of randomness because their presence and behaviour at carcasses is not uniform (Devault et al., 2003). Invertebrate scavengers typically colonise most carcasses but may react to the presence or absence of vertebrate scavengers, or how much carcass biomass remains following vertebrate scavenging. This is exemplified in a recent experiment in South-eastern Spain by Muñoz-Lozano et al where the succession of insects changed in the absence of vertebrate scavengers on carnivore carcasses (Muñoz-Lozano et al., 2019). Thus, understanding how these scavenger guilds interact with each other at carrion is integral to shaping our understanding of food web dynamics around carrion.

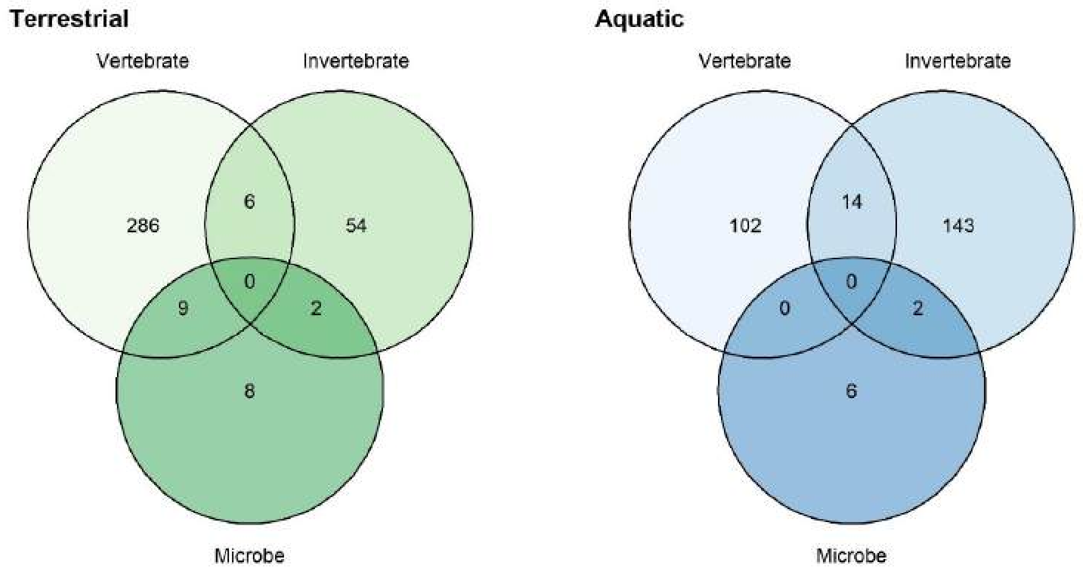

Figure 5: The number of publications on different scavenger guilds in terrestrial and aquatic ecosystems from the search results of Figure 4. Note the relatively low number of studies that have assessed multiple scavenger guilds, including vertebrates and invertebrates.

Scavenging's Role in Ecological Systems

Scavenging is an intricate and dynamic part of that nutrient flow in that it provides benefits both at the local and landscape levels through the recycling of deceased animal tissue (O'Bryan et al., 2018). Scavenging has two direct and distinct roles: 1) the consumption of carrion as a resource as individual scavengers compete for nutrients, and 2) the dispersal of nutrients throughout the ecosystem. Locally, scavengers benefit from the direct consumption of carrion as a resource while at an ecosystem level nutrients are then disbursed by scavengers by excretion or by becoming prey or detritus themselves (Moleón et al., 2019).

An artifact of nutrient flows in natural systems is a recycling of detritus by living organisms (Carter et al., 2007; Olea et al., 2019b). Scavenging occupies a niche of that energy flow defining itself to be the consumption of deceased animal tissues by other animals and microorganisms (Olea et al., 2019b). Carrion is often a necessary resource for many species that either subsist entirely on it (obligate) or supplement large portions of their diet with it (facultative) (Moleón et al., 2014). In many instances carrion is often a more readily available resource for carnivorous animals than live prey and thus scavenging is an integral part in all complex food webs (Moleón et al., 2014).

Species appearing at carcasses can be categorised into functional groups (e.g. microbes, invertebrates, vertebrates) that operate competitively and mutualistically for the duration of the decomposition (Olea et al., 2019a). These functional groups decompose detritus by 1) breaking down material at a cellular level, 2) removing biomass, and 3) increasing carcass fragmentation and facilitating access (Barton et al., 2019; DeVault et al., 2003; Lauber et al., 2014; Payne, 1965; Pechal et al., 2014; Wilson and Wolkovich, 2011). The services these scavengers provide in the process of removing carrion are complimentary and additive. Disruptions to the intactness of the scavenger guilds has been shown to increase carcass persistence (Hill et al., 2018; Lauber et al., 2014; Pechal et al., 2014). Thus, to maintain the efficient removal of carrion as a functional ecosystem service, an intact and diverse assemblages of scavenger guilds is needed.

The study of scavenging in Australian terrestrial systems is particularly important due to an overabundance of carrion relative to its available scavenging guilds (Barton et al., 2013; Read and Wilson, 2004). People are reliant on the natural processes of decomposition for removal of animal detritus despite having negative relationships with the species that carry out the process (Markandya et al., 2008; O'Bryan et al., 2018). With the advent of western colonisation of Australia, the rise of carrion likely increased as a result of agricultural and land management practices requiring control of wild and feral "pest species" (Cook and Jovanović, 2019; Hrdina, 2014; Lawrence and Davies, 2011). This practice of culling "pest species" continues and has only increased; just within New South Wales the last reported take of large macropods (Eastern Grey, Western Grey, and Red Kangaroo) in 2018 was 467,456 individuals (Environment, Energy and Science, 2019). This cultural phenomenon means millions of kilograms of terrestrial heterotrophic biomass is left in fields for nature to decompose. This creates a complex situation between people and wildlife as scavenging species attempt to utilise this resource while it creates possible hubs of disease transmission and attracts species people commonly have conflict with (e.g., the dingo: *Canis lupus dingo,* red fox: *Vulpes vulpes*, and feral cat: *Felis catus*). Although many species that scavenge are not favorited by livestock practitioners, their effects at removing diseased carcasses, and in turn any carcass borne pathogens, from the landscape can provide a beneficial effect (Vicente and VerCauteren, 2019). In a case study, vultures endemic to India had a significant reduction in the number of rabies cases in humans by reducing the availability of livestock carcasses to infected feral dogs (Markandya et al., 2008). Vulture scavenging reduced a need for rabies vaccinations in remote villages producing a significant economic benefit for the rural community.

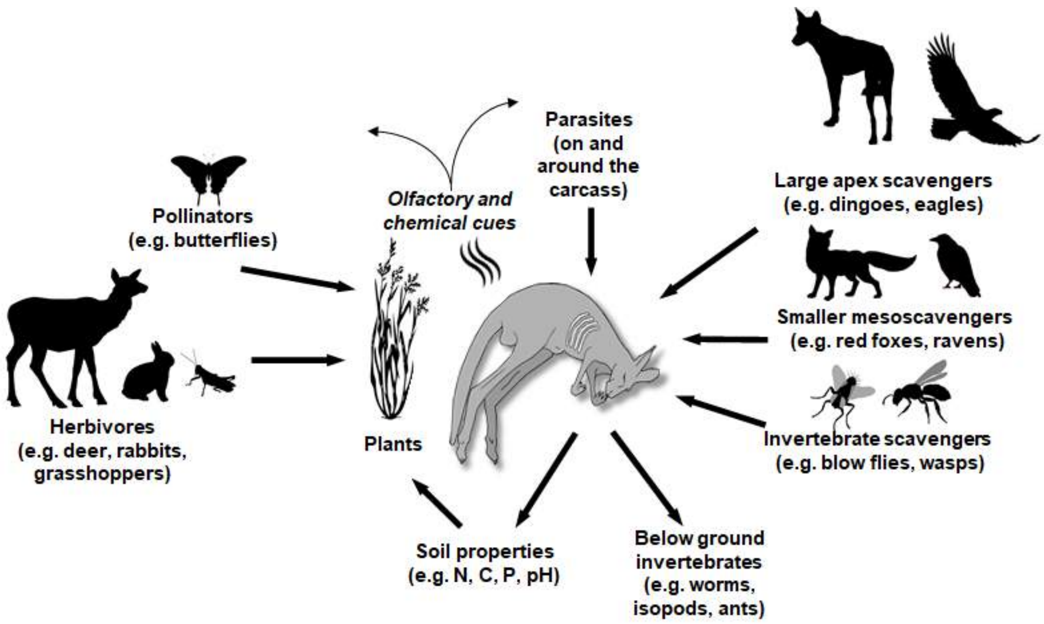

Figure 6: A conceptual carrion-centric food-web of Kosciuszko NP with arrows from scavengers and herbivores/pollinators indicating feeding events, and arrows from carrion indicating nutrient flow that affects other components of the ecosystem. Carcasses supply nutrients to a broad taxonomic range including plants, microbes, invertebrates, and vertebrates. Actions by scavengers disperse nutrients away from the site in the form of scat or becoming carrion themselves. Plants adjacent to carcasses exhibit a growth response as soil receives the influx of these rare nutrients brought to them by microbes, invertebrates, and necrotic seepage. Aromatic particles diffuse from the carcass which are used by many scavengers as olfactory signal to locate carrion.

Processes of Decomposition

Decomposition of animal biomass is a dynamic and complex continual process that in terrestrial biomes is often characterised into distinct stages (Payne, 1965). I classified six stages (e.g.: autolysis, early or bloat, active, advanced, dry, and remains) following previously stated research by Payne (1965) and Carter et al. (2007). Each progression marks important changes that are happening to the carcass and are influenced by the assemblage and succession of scavenging guilds.

Autolysis or the "fresh" stage occurs rapidly after death as the lack of aerobic metabolism leads to a loss of homeostasis across cell membranes which rupture allowing the leakage of cellular enzymes that break down surrounding cells (Vass et al., 2002). Concurrently, microbes in the surrounding environment and within the carcass begin consuming the carcass, unhindered by a functioning immune system. Specialised invertebrate scavengers such as blow flies (Calliphoridae) and carrion beetles (Silphidae) appear rapidly to both deposit their eggs on the carcass' surface and consume it (Anderson et al., 2019). At this stage the carcass remains intact as it begins to be colonised by external scavenging communities that seek it out in response to the emanating gaseous by-products brought on by autolysis and microbial metabolism of tissue (Recinos-Aguilar et al., 2019).

As the carcass begins to change colour from early putrefaction and build-up gas within the body cavity, this marks the "bloat" or early stage. Internal pressures caused by the build-up of gasses from the cellular breakdown of the tissues cause the carcass to swell (Carter et al., 2007). This pressure releases fluids from within the carcass and in conjunction with scavenger activity (in most cases this may be maggot activity) causes ruptures in the flesh to relieve the pressure. The rupture of the cadaver expulses gasses containing aromatic particles and creates a large signal for scavengers that rely on olfactory cues to locate carrion. This also marks the next stage of decomposition.

The “active” stage is where the most rapid biomass loss occurs and the putrefaction of the soft tissues is visually apparent. This is often when insects and their larvae are at their most active. There are large releases of cadaveric fluid as the carcass ruptures from consumption. This release of fluid is a large influx of nutrients into the surrounding soil and forms the basis of what Carter et al (2007) refers to as the “cadaver decomposition island” (CDI). The CDI is a localised pulse of resources resulting from the decay of animal tissue. The duration of the active stage can depend heavily on the environmental conditions and the assemblage of scavengers that visit the carcass (Barton and Bump, 2019).

In the “advanced” stage, the carcass itself has very little soft tissue remaining and begins desiccating. Most of the nutrients from the carcass have been removed by scavengers dispersing it away from the carcass as they migrate away (Payne, 1965). The migration of maggots brought on by their pupation increases the radius of the CDI as they bring nutrients consumed at the carcass underground. This brings about a shift in insect assemblages leaving the semi-desiccated remains for beetles. There is still moisture and skin on the carcass as it slowly desiccates, fragments, and approaches disintegration.

At the "dry” decay stage the cadaver is completely desiccated and its remaining connective skin tissue begins to fray due to natural weathering (Barton and Bump, 2019). The carcass is fragmenting as pieces no longer held together by skin, sinew, and ligaments can separate. During this period a vegetation response may be seen bordering the radius of the CDI as plants utilise the nutrients brought underground during the “active” stage (Carter et al., 2007). The carcass progresses slowly through the “dry” stage as the quality of the carrion resource is depleted as it skeletonises.

Lastly, the corpse becomes “remains” as its fragments are removed, weathered, buried, and eventually, disintegrated. There is no distinct barrier marking this transition from “dry” to “remains” as it is a localised stochastic process that may take years (Carter et al., 2007). The final act of the decomposition marking its completion is the total disintegration and absorption of the remains into the ecosystem.

Terrestrial Scavenging Guilds

Figure 7: A pair of dingoes (*Canis lupus dingo*) feeding on a grey kangaroo (*Macropus giganteus*) carcass in Kosciuszko NP.

Roles of Microbial Scavengers

Microbes "kick-start" the decomposition process by breaking down the carcass on a cellular level (putrefaction) and releasing chemical cues which other scavenging guilds use to locate carrion (Carter et al., 2007). In most cases decomposition occurs almost immediately after the death of an organism (Payne, 1965). The halt of aerobic-metabolism brings about autolysis (the self-breakdown of enzymes and cellular material) and creates an environment suitable for anaerobic microorganisms to colonise and feed on tissue unhindered by a live-body's defensive mechanisms. Microbes are rapid colonisers of carrion because they are present at time of death in the organism and ubiquitously distributed in the environment. In some cases microbes can act as competitors and consumers of carrion by producing chemicals to deter animal scavengers (Burkepile et al., 2006).

Roles of Invertebrate Scavengers

Terrestrial Invertebrate scavengers, primarily insects, consume a significant amount of carrion biomass very rapidly; a process that is guided by their natural patterns of colonisation and succession (Anderson et al., 2019). It has been found in exclusionary experiments that insects have the ability to consume large terrestrial mammalian carcasses within a few days making their contribution to carrion removal not only important but extraordinary (Anderson et al., 2019; Barton and Evans, 2017; Payne, 1965; Pechal et al., 2014). Insects can specialise on specific types of tissue in carrion and their action on it creates availability to different assemblages throughout the carcass's use. Rapid colonisers, such as flies (Diptera) quickly locate carrion by following volatile cues (Kalinova et al., 2009; Recinos-Aguilar et al., 2019). This is followed by the development of maggot activity as fly eggs laid on the surface hatch and quickly attack the putrefying tissue. As the maggots develop, consuming and puncturing the carcass, slower colonisers such as beetles (Coleoptera) are drawn to the carrion (Archer, 2003; Bajerlein et al., 2011; Bourel et al., 1999). This process is dynamic with rapid action and consumption happening quickly after death and gradually declining as biomass depletes and putrefies. This process of colonisation and succession has been well documented in forensic sciences (Byrd and Tomberlin, 2019), but less so in natural settings.

Invertebrate patterns of colonisation of carcasses and succession are influenced by factors including climate, geography, seasonality, temperature, and aromatic particles (Anderson et al., 2019). Changes to these parameters influence carcass persistence by effecting the behaviour of insect activity and discovery of carrion (Mellanby, 1939; Merritt and Jong, 2015). In colder latitudes, higher altitudes, or winter, for instance, there tends to be lower insect activity in part because of their average colder temperatures. This may delay or prevent insect activities on carcasses slowing the removal of biomass by insects (Archer, 2004; George et al., 2013; KR Norris, 1966). Conversely, carcasses are progressed more rapidly by insects and their larvae at higher temperatures (Archer, 2004). Because of temperature dependence, trends of insect colonisation on carcasses follow seasonal patterns and can affect cadaver decomposition (Archer, 2003; Benbow et al., 2013). Insects tend to have more rapid colonisation and be more abundant and active on cadavers in warmer months (Archer, 2003). This has a direct effect on decay rate as carcasses with less insect activity persist longer (Benbow et al., 2013; Payne, 1965). Additionally, vertebrate scavenge guilds provide localised variation in decomposition when they compete with insects to consume carrion.

Figure 8: Examples of necrophilous insects of Kosciuszko NP. In order of appearances from left to right: carrion beetles (Silphidae), blow flies (Calliphoridae), maggots (larval Calliphoridae), ants (Formicidae), European wasp (Vespidae), and blow fly (Calliphoridae).

Roles of Vertebrate Scavengers

Vertebrates can efficiently remove carcass biomass in many ecosystems (DeVault et al., 2003). Their interactions with carcasses tend to accelerate decomposition because they remove both carcass tissue and bones (Parmenter and MacMahon, 2009). The remaining carcass after vertebrate consumption is often quite fragmented and exposed leaving the remains more easily accessible to invertebrate scavengers which tend to have more difficulty in reaching the internals of undisturbed detritus. Nutrients from vertebrates feeding on carrion is dispersed further as they remove fragments and bones from the carcass and deposit them via their scats. The assemblage of vertebrate species influences decay rate as larger carnivores can dominate carcasses thereby influencing the community structure of other species feeding on the carcass (Wilson and Wolkovich, 2011). For example, areas where Tasmanian devils (*Sarcophilus harrisii*) were suppressed had a 2.6-fold higher carcass persistence and meso-scavenger species had higher usage (Cunningham et al., 2018). Thus, the Tasmanian Devil is an apex scavenger whose influence over other scavengers structures the necrophilous community and reduces carrion persistence. Likewise, in Spain, vertebrate scavenging was found to influence invertebrate community succession as vertebrates removed carcasses and in turn altered successional cues (Munoz-Lozano et al., 2019). Carcasses fed upon by vertebrates had lower diversity of beetle and fly species.

Figure 9: An example of the vertebrate facultative scavenger guild of Kosciuszko NP. In order of appearance from left to right: wedge-tailed eagle (*Aquila audax*), dingo (*Canis lupus dingo*), red fox (*Vulpes vulpes*), Australian raven (*Corvus coronoides*), feral pig (*Sus scrofa*), brushtail possum (*Trichosurus vulpecula*), feral cat (*Felis catus*). Red fox, feral pig, and feral cat are all exotic facultative scavengers in Australian ecosystems.

Functional Redundancy

Vertebrate and insect scavengers' ability to remove carcass biomass and the competition between them provides functional redundancy in ecosystems capacity to remove carrion. By definition, functional redundancy implies that species loss is compensated by other species contributing similarly to functioning (Fetzer et al., 2015). This is particularly important with respect to carrion removal as variation in the colonisation and assemblage of species can change between carcasses, but the result should ideally be the same in a functioning/healthy ecosystem e.g.: rapid removal of carcass biomass. Thus, the resilience of an ecosystem can be measured by how long carcass persist in the landscape (Cardinale et al., 2006). For example, if there is a reduction in the abundance of an apex scavenger in an ecosystem one expects to either see 1) a change in the ecosystem functionality or 2) other species providing the same function (Biggs et al., 2020; Naeem, 1998; Rosenfeld, 2002; van der Plas, 2019). In the second case there is a functional redundancy with the ecosystem service at which the roles of the apex predators are being supplied by alternative species (Lawton and Brown, 1994). Having such redundancies provides ecosystem resilience (Naeem, 1998).

In terms of terrestrial carcass removal, functional redundancy is dependent on specific functionalities from a scavenger assemblage rather than species richness (Biggs et al., 2020). This means the capacity to remove carrion is dependent on specific key species rather than all species because not all species consume equal quantities of carcass. In an Australian study by Huijbers et al (2015) of carrion removal in coastal beach ecosystems by vertebrates, the suppression of the main functional group (raptor species) by urbanisation greatly increased carcass persistence because terrestrial vertebrates (i.e. canids) were unable to remove as many. Thus, the assemblage of scavengers had a great effect on ecosystem functionality. In a study of functional redundancy of plant species by Fonesca and Ganada (2001) of South American flora, they estimated that local extinctions could remove up to 75% of floral species before there was a loss of functional groups. Thus, the loss of a functional group has greater impact on ecosystem resilience than a broad-ranging reduction of species richness. This means that ecosystems with many functional groups can tolerate extinction events better than ecosystems with few independent of species richness. Therefore, the understanding of how each functional group lives and operates is vital to future predictions and management of ecosystems (Rosenfeld, 2002).

In Australia, there is a need to understand the functionality of scavenging species as agricultural practices in favour of growing livestock have drastically reduced some facultative scavengers like dingoes, while creating an overabundance of native macropods (Environment, Energy and Science, 2019). The effect of suppressing vertebrate scavengers, such as dingoes, has on carcass persistence is not well studied but could possibly be destabilising localised vertebrate community structures thus altering food-webs (Cardinale et al., 2006; Huijbers et al., 2015; Wilson and Wolkovich, 2011). With the decline of larger vertebrate scavengers, the resiliency of this ecosystem service potentially lies with smaller vertebrate scavengers, insects, and microbial scavenging guilds to compensate for the loss.

Alpine Australia

The Australian alpine comprises approximately 250,000 hectares of rugged mountainous terrain (Costin, 2000). The alpine and sub-alpine surrounding it are rare and distinguished environments that holds immense ecological and socio-economic value (New South Wales et al., 2006). Located in South-eastern Australia on the border of New South Wales and Victoria, it is the highest elevation of the Australian land mass and the only part that receives consistent annual snowfall. It is this unique attribute and its consequent ecosystems that have earned Kosciuszko NP its place in the international community as a biodiversity hotspot as well as the source of millions of dollars of economic output annually (Snowy Monaro Regional Council, 2018; Snowy Valleys Council, 2018; United Nations Educational, Scientific and Cultural Organization, 2015).

Ecological Value

The Australian Alps' ecosystems provide many scientific and ecological benefits all while supporting a highly unique habitat to some of Australia's most rare flora and fauna. In a 2006 Department of Environment management plan, it was stated by the World Conservation Union that the Australian Alps is a centre for biodiversity and its endemism "is amongst the highest for any mountain area in the world" (New South Wales et al., 2006). Since the uplift of Australia's Great Dividing Range and the consequent formation of what we know as the Snowy Mountains (Müller et al., 2016; Strom, 2016), species have colonised this montane region and many lived in seclusion allowing for unique adaptations radically different than the rest of the continent (Costin, 2000). The alpine and subalpine ecotones are structured around peat-bogs, fens, and snow-gum forests that moderate alpine and subalpine hydrology and provide habitat to some of Australia's most rare and unique species as well as large herbivorous mammals (Costin, 2000; New South Wales et al., 2012).

The mires and fens of the alps moderate water flow and retention and filter out sediment resulting in longer retention and dispersion of clearer water (New South Wales et al., 2012). The flora of these bogs is effective at retaining snowmelt and filtering out particulate matter, allowing water to diffuse into the soil while creating a seal to retain ground water. This is important as the lack of these peat-forming bogs reduces runoff regulation into surface-flowing water creating a more erratic and muddy water supply (Wimbush and Costin, 1983). Another property of these alpine wetlands is their ability to sequester and store carbon (New South Wales et al., 2012).

The alpine wetlands capture sedimentary carbon through the growth of associated vegetation and the deposition of particles (Hope et al., 2019). In a technical report published by the Office of

Environment and Heritage (2012) they report the entire area of wetlands “in the Snowy Mountains region total 7,985 [hectares], of which 6,037 [hectares] is in Kosciuszko National Park” which stores an estimated 3.55 million tonnes of carbon and has approximate annual sequestration rate of 4,950 t C/year (New South Wales et al., 2012). These wetland ecosystems alongside adjacent subalpine forested environments create a biodiversity hotspot featuring some of Australia’s most rare and unique fauna and flora (Steffen et al., 2009).

The Australian Alps is home to a plethora of endemic threatened and endangered species such as the broad toothed rat (*Mastacomys fuscus*), Mountain pygmy possum (*Burramys parvus*), and Southern corroboree frog (*Pseudophryne corroboree*). The scarcity and isolation of high elevation among one of the lowest, flattest land masses has enabled unique adaptations among many alpine species (Steffen et al., 2009) earning its recognition to the international community as a biodiversity hotspot (United Nations Educational, Scientific and Cultural Organization, 2015). The Australian Alps’ climate and biodiversity have also provided many scientific opportunities as this offers a comparative environment and ecosystem to those more commonly found in the northern hemisphere (Mansergh et al., 2003; United Nations Educational, Scientific and Cultural Organization, 2015). However, its uniqueness and rarity make Australian alpine fauna and flora vulnerable to outside environmental and anthropogenic pressures (Wyborn, 2009).

Landscape level changes to the Snowy Mountains such as climate change, feral species invasions, livestock production, and wildfires often have a profound disruptive effect on the local ecology and biodiversity (Green and Pickering, 2002; Steffen et al., 2009). Disruptions to the local biodiversity have potential to impact ecosystem services and interrupt its functionality (Mace et al., 2012; van der Plas, 2019). Despite the Australian Alps’ vulnerabilities to change, it generates tremendous economic value derived from its environment and its ecosystems.

Economic Value

Not only are the Snowy Mountains’ ecosystems and geology intrinsically valuable, but they also hold a large economic value through tourism, power-generation, water disbursement, and near-by agricultural production. Tourism alone in fiscal year 2019-2020 generated a gross value added of $389 million to the Snowy Monaro region (Tourism Research Australia, 2020). This includes activities directly reliant on alpine ecosystems such as skiing and mountain biking.

Power generation via The Snowy Hydro-Electric Scheme relies on surface water from the alpine to generate 4,500 gigawatt-hours per year. This energy supplies a significant amount electricity to New South Wales, Victoria, and the Australian Capital Territory (Australian Bureau of Statistics, 2012; Snowy Hydro Limited, n.d.). Snowmelt and rainfall also feed some of Australia’s largest rivers, the Murray and the Murrumbidgee. This is approximately 4,000 gigalitres of water per year that supplies many important agricultural sectors including 50% of Australia's rice production and 42% of New South Wales's fruit production (Murray-Darling Basin Authority, 2015).

This rugged, rural part of Australia has been heavily grazed by livestock since western settlement (Costin, 2000). Although Kosciuszko NP itself prohibits livestock grazing, the surrounding private lands are largely still livestock operations (Scherrer and Pickering, 2005). Many private livestock operations adjacent to the park manage for "pest" species (Costin, 2000). Starting with western settlement and continuing today, macropods and associated predators are culled to reduce production disruption (Environment, Energy and Science, 2019). Although this may be a viable solution for a short term with a narrow, localised effect, this creates a surplus of carrion adjacent to national park borders and may reduce vertebrate scavenger abundance.

The Snow Mountains also offers unique scientific comparisons between alpine regions on other continents. Kosciuszko National Park's temperate nature makes this an ideal place to study ecology with an Australian context as it resembles both environments rigorously studied in the northern hemisphere with an assemblage of unique native flora and fauna (Mansergh et al., 2003). This allows a closer comparison of ecological processes studied in northern hemisphere environments directly to the unique species of Australia. Discoveries made here highlight just how unique, rare, and distinct Australia's ecosystem assemblage is.

Current Carrion Management in the High Country

The current management plan for Kosciuszko National Park, enacted by the National Parks and Wildlife Service in 2006, has conservation objectives that call for "the restoring and protecting the significant environmental values of the park" (New South Wales et al., 2006) including objectives of removing introduced fauna where feasible (11.4.1) and doing so in a humane manner (11.4.3). These conservation objectives encapsulate the management of large exotic herbivores allowing for control methods that are within the scope of the (*Prevention of Cruelty to Animals Act*, 1997). An additional management plan for the control of feral horses follows similar conservation guidelines to mitigate their adverse effects on endemic flora and fauna but not fully remove them from Kosciuszko National Park (New South Wales National Parks and Wildlife Service et al., 2021). In the plan, feral horse populations are to be reduced from their existing size (an estimate of 14,380 ($CI_{95\%}$ = 8,798 – 22,555)(Cairns, 2020)) to 3,000 and contained to a designated 32% of the total area of Kosciuszko National Park. Carcasses from lethal control will be managed 'on-site' and their disposal will be considered on a 'case-by-case' basis with no defined methodology (New South Wales National Parks and Wildlife Service et al., 2021). The plan does not require any action to be taken to mitigate the influx of carcasses created as a result of lethal control but does acknowledge that the “[d]isposal of carcasses presents logistical challenges” to adequately manage (New South Wales National Parks and Wildlife Service et al., 2021).

The current management plans for Kosciuszko National Park explicitly state for the reduction or removal of feral fauna in an effort to maintain pre-European settlement biodiversity (New South Wales et al., 2006; New South Wales National Parks and Wildlife Service et al., 2016). This includes large culling efforts by the National Parks and Wildlife Service and adjacent private stake holders to control introduced herbivores and reduce competition with grazing livestock. Although, the control of invasive herbivores in Kosciuszko National Park is not new, the effects of the carrion in the Park as a result of these actions are not well documented. These lethal controls may artificially increase the biomass of carrion in the local environment and create opportunities for scavengers. However, effects of the influx of carrion from human-caused mortalities and the true quantity of large mammalian carcasses into this biodiverse and fragile environment are understudied.

Understanding Kosciuszko’s Necrobiome

Currently there is limited knowledge of what assemblage of fauna use carrion in Kosciuszko National Park. Intertwined in this is a seasonal component as the temperate nature of the area brings out annual trends in the flora and fauna (e.g.: insects are less active in the winter, invasive European wasps appear in mass in autumn, and seasonal effects on local apex scavengers are not well documented). There are known negative effects that arise from carcasses in Kosciuszko—such as exclusive competition and colonisation by invasive European wasps (Spencer et al., 2020)—so understanding natural cycles of carrion and its necrobiome can inform management decisions to mitigate potential threats.

In this study, I attempt to fill in some knowledge gaps relating to Kosciuszko National Park’s necrobiome by assessing the link between scavenging guilds and their contributions to reducing carcass persistence. Understanding the underlying ecology surrounding this process will inform management about the mechanisms of Kosciuszko National Park’s necrobiome and shed light on how functionally resilient it is (in terms of the capacity of the scavenger guild to remove carcasses from the landscape). Many studies globally focus on single guilds of scavengers but do not address the competition they have with one another in a comprehensive way (Barton et al., 2013). This is indeed a knowledge gap because competition for rare resources such as carrion between vertebrates, insects, and microbes can influence carcass persistence (DeVault et al., 2003). It is already known that the exclusion of vertebrates and/or insects can slow decay (Barton and Evans, 2017; Hill et al., 2018; Payne, 1965; Pechal et al., 2014; Turner et al., 2020) but the functional capacity for one of these guilds to compensate for the suppression of another is not known. In essence, the following key questions remain:

Q1: How much does each scavenging guild contribute to carrion removal?

Q2: Can the insect scavenging guild compensate for the loss of a vertebrate scavenging guild?

Q3: How do insects respond to the absence of vertebrate scavengers?

To answer these questions, this study has broken them into two chapters examining the persistence of large mammalian carcasses in response to the experimental restriction of vertebrate and insect scavenging guilds. If each of these scavenger guilds plays a functional scavenging role, then we would expect to see shorter carcass persistence where there is the least number of guilds restricted. If there is competition between vertebrates and insect scavengers, then we would expect to see a change in insect assemblages where vertebrates are excluded.

The first data chapter focuses on carcass persistence across three separate scavenger exclusion treatments (open: no exclusion, cage: vertebrate exclusion, and cage + mesh: vertebrate + insect exclusion) across four different seasons. The broad prediction is increased (prolonged) carcass persistence with scavenger exclusion, with the longest persistence seen for the vertebrate + insect exclusion (Figure 10). The methodological approach adopted not only provides a characterisation of the contribution of each scavenger guild but also a measure of the functional redundancy between guilds—an indicator of the resilience of an ecosystem service (Lawton and Brown, 1994; Naeem, 1998).

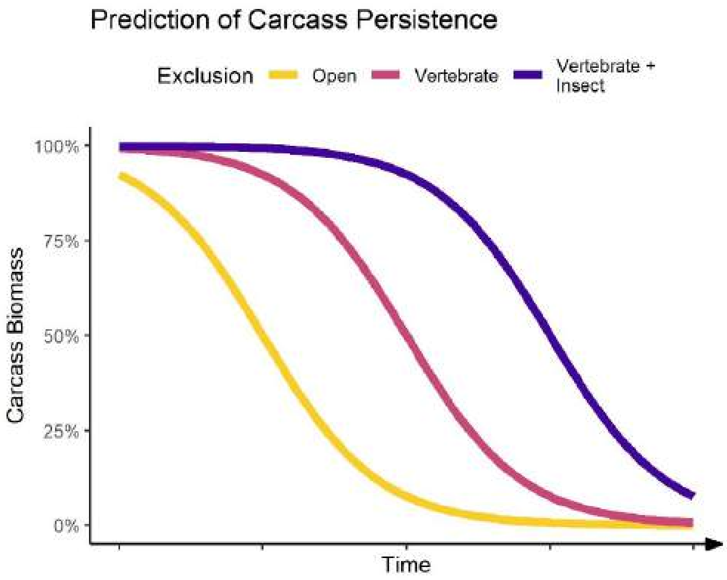

Figure 10: Predicted carcass persistence following experimental restriction of scavenger guilds to kangaroo carcasses. Note the vertebrate exclusion treatment allows insect and microbial scavenger access. The vertebrate + insect exclusion treatment allows only microbial scavengers.

The second chapter focuses on insect responses to vertebrate exclusion during the summer period when insect activity is at its peak. Both vertebrate and insect scavenger guilds provide a vital ecosystem service by removing carrion biomass, but in many ecosystems they are in direct competition with each other for resources (DeVault et al., 2003; Moleón et al., 2015; Ray et al., 2014). The broad prediction is that in the absence of vertebrate scavengers, insects will colonise and dominate carcasses in greater abundance and diversity due to the lack of disruptions caused by vertebrates feeding (Figure 11).

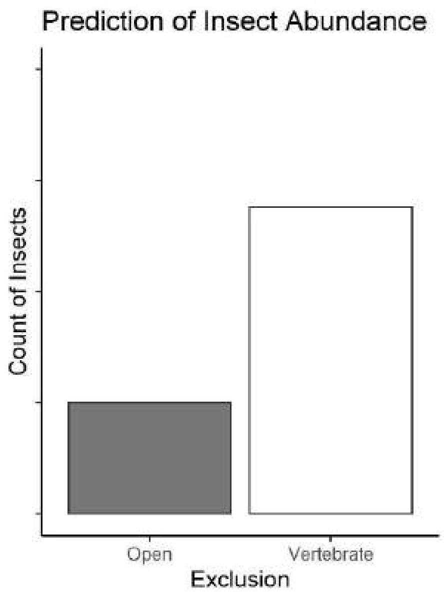

Figure 11: Predicted insect abundance following the experimental restriction of vertebrate scavengers.

References

Anderson, G.S., Barton, P.S., Archer, M., Wallace, J.R., 2019. Invertebrate Scavenging Communities, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 45–69. https://doi.org/10.1007/978-3-030-16501-7_3

Archer, M.S., 2004. Rainfall and temperature effects on the decomposition rate of exposed neonatal remains. Sci Justice 44, 35–41. https://doi.org/10.1016/S1355-0306(04)71683-4

Archer, M.S., 2003. Annual variation in arrival and departure times of carrion insects at carcasses: implications for succession studies in forensic entomology. Aust. J. Zool. 51, 569. https://doi.org/10.1071/ZO03053

Australian Bureau of Statistics, 2012. The Snowy Mountains Hydro-Electric Scheme [WWW Document]. Australian Bureau of Statistics. URL https://www.abs.gov.au/ausstats/abs@.nsf/0/FDE81AE268C76207CA2569DE00274C14?Open# (accessed 8.16.21).

Bajerlein, D., Matuszewski, S., Konwerski, S., 2011. Insect succession on carrion: Seasonality, habitat preference and residency of histerid beetles (Coleoptera: Histeridae) visiting pig carrion exposed in various forests (Western Poland). Polish Journal of Ecology 59, 789–797.

Barton, P.S., Bump, J.K., 2019. Carrion Decomposition, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 101–124. https://doi.org/10.1007/978-3-030-16501-7_5

Barton, P.S., Cunningham, S.A., Lindenmayer, D.B., Manning, A.D., 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia 171, 761–772. https://doi.org/10.1007/s00442-012-2460-3

Barton, P.S., Evans, M.J., 2017. Insect biodiversity meets ecosystem function: differential effects of habitat and insects on carrion decomposition. Ecological Entomology 42, 364–374. https://doi.org/10.1111/een.12395

Barton, P.S., Evans, M.J., Foster, C.N., Pechal, J.L., Bump, J.K., Quaggiotto, M.-M., Benbow, M.E., 2019. Towards Quantifying Carrion Biomass in Ecosystems. Trends in Ecology & Evolution 34, 950–961. https://doi.org/10.1016/j.tree.2019.06.001

Beasley, J.C., Olson, Z.H., DeVault, T.L., 2015. Ecological role of vertebrate scavengers. CRC Press. https://doi.org/10.1201/b18819

Benbow, M., Barton, P., Ulyshen, M., Beasley, J., DeVault, T., Strickland, M., Tomberlin, J., Jordan, H., Pechal, J., 2019. Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. Ecological Monographs 89. https://doi.org/10.1002/ecm.1331

Benbow, M., Lewis, A., Tomberlin, J., Pechal, J., 2013. Seasonal Necrophagous Insect Community Assembly During Vertebrate Carrion Decomposition. Journal of Medical Entomology 50, 440–450. https://doi.org/10.1603/ME12194

Benbow, M.E., Tomberlin, J.K., Tarone, A.M. (Eds.), 2015. Carrion Ecology, Evolution, and Their Applications. CRC Press, Boca Raton. https://doi.org/10.1201/b18819

Biggs, C.R., Yeager, L.A., Bolser, D.G., Bonsell, C., Dichiera, A.M., Hou, Z., Keyser, S.R., Khursigara, A.J., Lu, K., Muth, A.F., Negrete, B., Erisman, B.E., 2020. Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. Ecosphere 11, e03184. https://doi.org/10.1002/ecs2.3184Bourel, B., Martin-Bouyer, L., Hedouin, V., Cailliez, J., Derout, D., Gosset, D., 1999. Necrophilous insect succession on rabbit carrion in sand dune habitats in northern France. Journal of Medical Entomology 36, 420–425. https://doi.org/10.1093/jmedent/36.4.420

Burkepile, D., Parker, J., Woodson, C., Mills, H., Kubanek, J., Sobecky, P., Hay, M., 2006. Chemically mediated competition between microbes and animals: Microbes as consumers in food webs. Ecology 87, 2821–2831. https://doi.org/10.1890/0012-9658(2006)87[2821:CMCBMA]2.0.CO;2

Byrd, J.H., Tomberlin, J.K. (Eds.), 2019. Forensic Entomology: The Utility of Arthropods in Legal Investigations, 3rd ed. CRC Press, Boca Raton. https://doi.org/10.4324/9781351163767

Cardinale, B., Srivastava, D., Duffy, J., Wright, J., Downing, A., Sankaran, M., Jouseau, C., 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443, 989–92. https://doi.org/10.1038/nature05202

Carter, D.O., Yellowlees, D., Tibbett, M., 2007. Cadaver decomposition in terrestrial ecosystems. Naturwissenschaften 94, 12–24. https://doi.org/10.1007/s00114-006-0159-1

Charabidze, D., Trumbo, S., Grzywacz, A., Costa, J.T., Benbow, M.E., Barton, P.S., Matuszewski, S., 2021. Convergence of Social Strategies in Carrion Breeding Insects. BioScience 71, 1028–1037. https://doi.org/10.1093/biosci/biab068

Cook, R., Jovanović, S., 2019. The Emu Strikes Back: An Inquiry into Australia's Peculiar Military Action of 1932. Romanian Journal of Historical Studies 2, 1–11.

Costin, A.B., 2000. Kosciuszko alpine flora, 2nd ed. ed. CSIRO Publishing, Melbourne.

Crippen, T.L., Benbow, M.E., Pechal, J.L., 2015. Microbial Interactions during Carrion Decomposition, in: Carrion Ecology, Evolution, and Their Applications. CRC Press.

Cunningham, C.X., Johnson, C.N., Barmuta, L.A., Hollings, T., Woehler, E.J., Jones, M.E., 2018. Top carnivore decline has cascading effects on scavengers and carrion persistence. Proceedings. Biological sciences 285. https://doi.org/10.1098/rspb.2018.1582

DeVault, T.L., Jr, O.E.R., Shivik, J.A., 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102, 225–234. https://doi.org/10.1034/j.1600-0706.2003.12378.x

Devault, T.L., Rhodes, O.E., Shivik, J.A., Devault, T.L., Rhodes, O.E., Shivik, J.A., 2003. Scavenging by Vertebrates : Behavioral , Ecological , and Evolutionary Perspectives on an Important Energy Transfer Pathway in Terrestrial Ecosystems Published by : Wiley on behalf of Nordic Society Oikos Stable URL : http://www.jstor. Oikos 102, 225–234.

Environment, Energy and Science, 2019. 2020 Quota Report New South Wales Commercial Kangaroo Harvest Management Plan 2017-21. Department of Planning, Industry and Environment.

Evans, M., Wallman, J., Barton, P., 2020. Traits reveal ecological strategies driving carrion insect community assembly. Ecological Entomology 45, 966–977. https://doi.org/10.1111/een.12869

Fetzer, I., Johst, K., Schäwe, R., Banitz, T., Harms, H., Chatzinotas, A., 2015. The extent of functional redundancy changes as species' roles shift in different environments. PNAS 112, 14888–14893. https://doi.org/10.1073/pnas.1505587112

Fonseca, C.R., Ganade, G., 2001. Species functional redundancy, random extinctions and the stability of ecosystems. Journal of Ecology 89, 118–125. https://doi.org/10.1046/j.1365-2745.2001.00528.x

George, K.A., Archer, M.S., Toop, T., 2013. Abiotic environmental factors influencing blowfly colonisation patterns in the field. Forensic Science International 229, 100–107. https://doi.org/10.1016/j.forsciint.2013.03.033

Golding, D., 2019. The man from snowy river. Metro 114–123. https://doi.org/10.3316/ielapa.241867357938157

Green, K., Pickering, C.M., 2002. A Scenario for Mammal and Bird Diversity in the Snowy Mountains of Australia in Relation to Climate Change, in: Mountain Biodiversity. Routledge.

Hill, J.E., DeVault, T.L., Beasley, J.C., Rhodes, O.E., Belant, J.L., 2018. Effects of vulture exclusion on carrion consumption by facultative scavengers. Ecology and Evolution 8, 2518–2526. https://doi.org/10.1002/ece3.3840

Hope, G., Mooney, S.D., Allen, K., Baker, P., Keaney, B., Kemp, J., Martin, L., Pearson, S., Stevenson, J., Zheng, X., 2019. Science through time: Understanding the archive at rennix gap bog, a sub-alpine peatland in kosciuszko national park, New South Wales, Australia. Proceedings of the Linnean Society of New South Wales 141, 25–47.

Hrdina, F., 2014. Marsupial destruction in Queensland 1877-1930. Australian Zoologist 30, 272–286. https://doi.org/10.7882/AZ.1997.003

Huijbers, C.M., Schlacher, T.A., Schoeman, D.S., Olds, A.D., Weston, M.A., Connolly, R.M., 2015. Limited functional redundancy in vertebrate scavenger guilds fails to compensate for the loss of raptors from urbanized sandy beaches. Diversity and Distributions 21, 55–63. https://doi.org/10.1111/ddi.12282

Kalinova, B., Podskalska, H., Ruzicka, J., Hoskovec, M., 2009. Irresistible bouquet of death-how are burying beetles (Coleoptera: Silphidae: Nicrophorus) attracted by carcasses. Naturwissenschaften 96, 889–899. https://doi.org/10.1007/s00114-009-0545-6

KR Norris, 1966. Daily patterns of flight activity of blowflies (Calliphoridae : Diptera) in the Canberra district as indicated by trap catches. Australian journal of zoology 14, 865–853. https://doi.org/10.1071/ZO9660835

Lauber, C.L., Metcalf, J.L., Keepers, K., Ackermann, G., Carter, D.O., Knight, R., 2014. Vertebrate Decomposition Is Accelerated by Soil Microbes. Appl. Environ. Microbiol. 80, 4920–4929. https://doi.org/10.1128/AEM.00957-14

Lawrence, S., Davies, P., 2011. An Archaeology of Australia Since 1788, Contributions To Global Historical Archaeology. Springer New York, New York, NY. https://doi.org/10.1007/978-1-4419-7485-3

Lawton, J.H., Brown, V.K., 1994. Redundancy in Ecosystems, in: Schulze, E.-D., Mooney, H.A. (Eds.), Biodiversity and Ecosystem Function, Praktische Zahnmedizin Odonto-Stomatologie Pratique Practical Dental Medicine. Springer, Berlin, Heidelberg, pp. 255–270. https://doi.org/10.1007/978-3-642-58001-7_12

Mace, G.M., Norris, K., Fitter, A.H., 2012. Biodiversity and ecosystem services: a multilayered relationship. Trends in Ecology & Evolution 27, 19–26. https://doi.org/10.1016/j.tree.2011.08.006

Mansergh, I., Newsome, A., Shorthouse, D., 2003. Fauna Values, in: An Assessment of the Values of Kosciuszko National Park. NSW National Parks and Wildlife Service, Queanbeyan NSW.

Markandya, A., Taylor, T., Longo, A., Murty, M.N., Murty, S., Dhavala, K., 2008. Counting the cost of vulture decline—An appraisal of the human health and other benefits of vultures in India. Ecological Economics, Special Section: Biodiversity and Policy 67, 194–204. https://doi.org/10.1016/j.ecolecon.2008.04.020

Mellanby, K., 1939. Low Temperature and Insect Activity. Proceedings of the Royal Society of London. Series B, Biological Sciences 127, 473–487.

Merritt, R.W., Jong, G.D.D., 2015. Arthropod Communities in Terrestrial Environments, in: Carrion Ecology, Evolution, and Their Applications. CRC Press.

Miller, G., 1982. The Man from Snowy River. Cambridge Productions Edgley International Snowy River Investment Pty. Ltd. The Hoyts Group, Australia.

Moleón, M., Sánchez-Zapata, J.A., Sebastián-González, E., Owen-Smith, N., 2015. Carcass size shapes the structure and functioning of an African scavenging assemblage. Oikos 124, 1391–1403. https://doi.org/10.1111/oik.02222

Moleón, M., Sánchez-Zapata, J.A., Selva, N., Donázar, J.A., Owen-Smith, N., 2014. Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. Biological Reviews 89, 1042–1054. https://doi.org/10.1111/brv.12097

Moleón, M., Selva, N., Quaggiotto, M.M., Bailey, D.M., Cortés-Avizanda, A., DeVault, T.L., 2019. Carrion Availability in Space and Time, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 23–44. https://doi.org/10.1007/978-3-030-16501-7_2

Müller, D., Seton, M., Zahirovic, S., Williams, S., Matthews, K., Wright, N., Shephard, G., Maloney, K., Barnett-Moore, N., Hosseinpour, M., Bower, D., Cannon, J., 2016. Ocean Basin Evolution and Global-Scale Plate Reorganization Events Since Pangea Breakup. Annual Review of Earth and Planetary Sciences 44, 107–138. https://doi.org/10.1146/annurev-earth-060115-012211

Muñoz-Lozano, C., Martín-Vega, D., Martínez-Carrasco, C., Sánchez-Zapata, J.A., Morales-Reyes, Z., Gonzálvez, M., Moleón, M., 2019. Avoidance of carnivore carcasses by vertebrate scavengers enables colonization by a diverse community of carrion insects. PLOS ONE 14, e0221890. https://doi.org/10.1371/journal.pone.0221890

Munoz-Lozano, C., Martin-Vega, D., Martinez-Carrasco, C., Sanchez-Zapata, J.A., Morales-Reyes, Z., Gonzalvez, M., Moleon, M., 2019. Avoidance of carnivore carcasses by vertebrate scavengers enables colonization by a diverse community of carrion insects. PLoS One 14, e0221890. https://doi.org/10.1371/journal.pone.0221890

Murray-Darling Basin Authority, 2015. Murrumbidgee [WWW Document]. Murray–Darling Basin Authority. URL https://www.mdba.gov.au/water-management/catchments/murrumbidgee (accessed 8.16.21).

Naeem, S., 1998. Species Redundancy and Ecosystem Reliability. Conservation Biology 12, 39–45.

New South Wales, Department of Environment and Conservation, Parks and Wildlife Division, New South Wales, Department of Environment and Conservation, 2006. Kosciuszko National Park plan of management: 2006. Dept. of Environment and Conservation NSW, Sydney South, N.S.W.

New South Wales, Office of Environment and Heritage, New South Wales National Parks and Wildlife Service, 2012. Peat-forming bogs and fens of the Snowy Mountains of NSW: technical report. Office of Environment and Heritage, Sydney South.

New South Wales National Parks and Wildlife Service, New South Wales, Department of Planning, I. and E., 2021. Kosciuszko National Park wild horse heritage management plan.Newsome, T.M., Barton, B., Buck, J.C., DeBruyn, J., Spencer, E., Ripple, W.J., Barton, P.S., 2021. Monitoring the dead as an ecosystem indicator. Ecology and Evolution 11, 5844–5856. https://doi.org/10.1002/ece3.7542

O'Bryan, C.J., Braczkowski, A.R., Beyer, H.L., Carter, N.H., Watson, J.E.M., McDonald-Madden, E., 2018. The contribution of predators and scavengers to human well-being. Nat Ecol Evol 2, 229–236. https://doi.org/10.1038/s41559-017-0421-2

Olea, P.P., Mateo-Tomas, P., 2009. The role of traditional farming practices in ecosystem conservation: The case of transhumance and vultures. BIOLOGICAL CONSERVATION 142, 1844–1853. https://doi.org/10.1016/j.biocon.2009.03.024

Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), 2019a. Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-030-16501-7

Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A., 2019b. Introduction to the Topic of Carrion Ecology and Management, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, José Antonio (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 1–20. https://doi.org/10.1007/978-3-030-16501-7_1

Parmenter, R.R., MacMahon, J.A., 2009. Carrion Decomposition and Nutrient Cycling in a Semiarid Shrub—Steppe Ecosystem. Ecological Monographs 79, 637–661.

Paterson, A.B. (Andrew B., Macarthur-Onslow, A.R., 2011. The man from Snowy River, [2011 edition]. ed, Australian children's classics. Angus & Robertson, Sydney, NSW.

Payne, J.A., 1965. A Summer Carrion Study of the Baby Pig Sus Scrofa Linnaeus. Ecology 46, 592–602. https://doi.org/10.2307/1934999

Pechal, J.L., Benbow, M.E., Crippen, T.L., Tarone, A.M., Tomberlin, J.K., 2014. Delayed insect access alters carrion decomposition and necrophagous insect community assembly. ECOSPHERE 5. https://doi.org/10.1890/ES14-00022.1

Pereira, L.M., Owen-Smith, N., Moleón, M., 2014. Facultative predation and scavenging by mammalian carnivores: Seasonal, regional and intra-guild comparisons. Mammal Review 44, 44–55. https://doi.org/10.1111/mam.12005

Ray, R.-R., H. Seibold, M. Heurich, 2014. Invertebrates outcompete vertebrate facultative scavengers in simulated lynx kills in the Bavarian Forest National Park, Germany. Animal biodiversity and conservation 37.

Read, J.L., Wilson, D., 2004. Scavengers and detritivores of kangaroo harvest offcuts in arid Australia. Wildl. Res. 31, 51. https://doi.org/10.1071/WR02051

Recinos-Aguilar, Y.M., García-García, M.D., Malo, E.A., Cruz-López, L., Rojas, J.C., 2019. The Colonization of Necrophagous Larvae Accelerates the Decomposition of Chicken Carcass and the Emission of Volatile Attractants for Blowflies (Diptera: Calliphoridae). Journal of Medical Entomology 56, 1590–1597. http://dx.doi.org.ezproxy.library.sydney.edu.au/10.1093/jme/tjz104

Rosenfeld, J.S., 2002. Functional redundancy in ecology and conservation. Oikos 98, 156–162. https://doi.org/10.1034/j.1600-0706.2002.980116.x

Scherrer, P., Pickering, C.M., 2005. Recovery of Alpine Vegetation from Grazing and Drought: Data from Long-term Photoquadrats in Kosciuszko National Park, Australia. Arctic, Antarctic, and Alpine Research 37, 574–584. https://doi.org/10.1657/1523-0430(2005)037[0574:ROAVFG]2.0.CO;2

Snowy Hydro Limited, n.d. The Snowy Scheme [WWW Document]. Snowy Hydro. URL https://www.snowyhydro.com.au/generation/the-snowy-scheme/ (accessed 8.16.21).

Snowy Monaro Regional Council, 2018. Snowy Monaro Regional Economic Development Strategy 2022 - Supporting Analysis.

Snowy Valleys Council, 2018. 2018 – 2022 Snowy Valleys Regional Economic Development Strategy 22.

Spencer, E.E., Barton, P.S., Ripple, W.J., Newsome, T.M., 2020. Invasive European wasps alter scavenging dynamics around carrion. Food Webs 24, e00144. https://doi.org/10.1016/j.fooweb.2020.e00144

Steffen, W.L., Natural Resource Management Ministerial Council (Australia), Biodiversity and Climate Change Expert Advisory Group (Australia), 2009. Australia's biodiversity and climate change: a strategic assessment of the vulnerability of Australia's biodiversity to climate change. Dept. of Climate Change, Canberra.

Strom, M., 2016. Kosciuszko explained: mystery of the Snowy Mountains solved [WWW Document]. The Sydney Morning Herald. URL https://www.smh.com.au/environment/kosciuszko-explained-mystery-of-the-snowy-mountains-solved-20160315-gnj2zg.html (accessed 9.15.21).

Tourism Research Australia, 2020. Regional Tourism Satellite Account 2019–20 | Tourism Research Australia [WWW Document]. Tourism Research Australia. URL https://www.tra.gov.au/data-and-research/reports/regional-tourism-satellite-account-2019-20/regional-tourism-satellite-account-2019-20 (accessed 8.16.21).

Turner, K.L., Conner, L.M., Beasley, J.C., 2020. Effect of mammalian mesopredator exclusion on vertebrate scavenging communities. Sci Rep 10, 2644. https://doi.org/10.1038/s41598-020-59560-9

United Nations Educational, Scientific and Cultural Organization, 2015. Kosciuszko | United Nations Educational, Scientific and Cultural Organization [WWW Document]. Ecological Sciences for Sustainable Development. URL http://www.unesco.org/new/en/natural-sciences/environment/ecological-sciences/biosphere-reserves/asia-and-the-pacific/australia/kosciuszko/ (accessed 5.28.21).

van der Plas, F., 2019. Biodiversity and ecosystem functioning in naturally assembled communities. Biological Reviews 94, 1220–1245. https://doi.org/10.1111/brv.12499

Vass, A., Barshick, S., Sega, G., Caton, J., Skeen, J., Love, J., Synstelien, J., 2002. Decomposition Chemistry of Human Remains: A New Methodology for Determining the Postmortem Interval. J. Forensic Sci. 47. https://doi.org/10.1520/JFS15294J

Vicente, J., VerCauteren, K., 2019. The Role of Scavenging in Disease Dynamics, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 161–182. https://doi.org/10.1007/978-3-030-16501-7_7

Wilmers, C.C., Getz, W.M., 2004. Simulating the effects of wolf-elk population dynamics on resource flow to scavengers. Ecological Modelling 177, 193–208. https://doi.org/10.1016/j.ecolmodel.2004.02.007

Wilmers, C.C., Post, E., 2006. Predicting the influence of wolf-provided carrion on scavenger community dynamics under climate change scenarios. Global Change Biology 12, 403–409. https://doi.org/10.1111/j.1365-2486.2005.01094.x

Wilson, E.E., Wolkovich, E.M., 2011. Scavenging: How carnivores and carrion structure communities. Trends in Ecology and Evolution 26, 129–135. https://doi.org/10.1016/j.tree.2010.12.011

Wimbush, D.J., Costin, A.B., 1983. Trends in drainage characteristics in the subalpine zone at Kosciusko.

Wyborn, C., 2009. Managing change or changing management: climate change and human use in Kosciuszko National Park. Australasian Journal of Environmental Management 16, 208–217. https://doi.org/10.1080/14486563.2009.9725236

Chapter 1

Insects drive carrion decomposition in a temperate montane environment

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Abstract

1. Ecosystems rely on scavengers to recycle and remove animal detritus. Resilient ecosystems should arguably contain diverse scavenger guilds that show capacity for functional redundancy such that the loss of species is compensated by other species contributing similarly to functioning.
2. Here, I examine the functional capacity of scavenging insects and facultative scavenging vertebrates to accelerate carcass biomass loss across different seasons, and whether the absence of vertebrate and insect scavenger guilds influence carcass persistence rates.
3. To do so, I measured carcass persistence (decay rates) of eastern grey kangaroos (*Macropus giganteus; 2,425kg*) over four seasons (autumn, winter, spring, and summer) in a subalpine ecosystem, including under different scavenger exclusion scenarios (i) vertebrate exclusion and (ii) vertebrate and insect exclusion.
4. I found limited functional redundancy in carcass consumption between vertebrate and insect scavengers. In summer, insects were the primary consumers of carrion biomass and were supplemented by occasional vertebrate scavenging. Colder seasons showed a complete lack of carrion removal by vertebrates in the absence of insects.
5. These results suggest there is a small timeframe in which carrion is removed quickly within the study area and that scavenging efficiency is primarily linked to the presence of insect scavengers. Facultative scavenging vertebrates in the study area may therefore have very limited capacity to accelerate carcass biomass loss, potentially necessitating the need to manage carcass loads under some circumstances.

Introduction

Scavenging of dead animal biomass (i.e. carrion) benefits ecosystems by recycling nutrients and sustaining biodiversity (Carter et al., 2007; O'Bryan et al., 2018). Scavenging is important as it 1) recycles nutrients back into ecosystems, 2) benefits the communities of organisms that consume it, and 3) removes otherwise harmful carcass-borne diseases (Barton et al., 2013; Beasley et al., 2012; Ogada et al., 2012; Wilson and Wolkovich, 2011). Maintaining scavenging as an ecosystem service is imperative for the functioning of healthy ecosystems as it sustains nutrient recycling (Barton et al., 2013; Benbow et al., 2015b, p. 3). Yet threats to biodiversity, including scavenger species, from human influences are increasing (Ogada et al., 2012; Ripple et al., 2014; Sebastián-González et al., 2019).

Threats to biodiversity could potentially result in a loss of species and their corresponding role in the ecosystem. This can undermine an ecosystem's ability to function, leaving a vulnerability to extinction events (Biggs et al., 2020; Cardinale et al., 2006; Huijbers et al., 2015). In terms of scavenging, resilient ecosystems should have the capacity to remove carrion and recycle their nutrients without disruption even under stress. This concept relies on overlap between scavenger's functional role to decompose carcasses (Biggs et al., 2020; Fonseca and Ganade, 2001). Thus, ecosystems with multiple redundant scavenging groups can theoretically sustain a localised extinction of a functional group and still decompose carrion efficiently. Scavengers may also have complimentary effects as well, such as vertebrates fragmenting carcasses allowing greater access for invertebrates. With complimentary effects, functional groups perform separate tasks in the decomposition process that are additive. However, in these cases the loss of a functional group would result in incomplete or inefficient decomposition, possibly extending carcass persistence. Thus, the combination of redundant and complimentary roles scavengers have with one another dictate the robustness and efficiency of an ecosystem's ability to decompose carrion (Rosenfeld, 2002).

Knowledge of functional redundancy among scavenger guilds and its consequence on the removal of carrion is limited (Biggs et al., 2020). To date, research has revealed that disruptions to scavenger assemblages reduce scavenging efficiency (Huijbers et al., 2015; Olson et al., 2012; Sugiura et al., 2013). However, many of these studies focus on narrow taxonomic interactions and the individual functional roles scavenging species have. It is known that vertebrate, invertebrate, and microbial scavenger guilds occupy complimentary functions in the decomposition process (Carter et al., 2007). In many cases these scavenger guilds operate in tandem often competing with one another for resources or facilitating decomposition (DeVault et al., 2004). Indeed, apex vertebrate scavengers in particular have the capacity to restructure community assemblages at carcasses amongst vertebrate meso-predators and insects, thus, affecting decay rate (Munoz-Lozano et al., 2019; Wilson and Wolkovich, 2011). Few studies have examined both vertebrate and insect scavenger guilds and therefore knowledge about the quantity of their redundant and complimentary functionality is lacking. This study seeks to fill that knowledge gap and characterise the redundant and complimentary functions vertebrate and insect scavengers have when decomposing carcasses to better understand their functional roles.

Carcass persistence (i.e. decay rate) is affected by interactions in and between scavenger guilds, but abiotic factors such as season, temperature, and humidity are also important (Carter et al., 2007; DeVault et al., 2004; Payne, 1965; Ray et al., 2014). Colder climates that offer a wide range of annual temperatures often have high variation in scavenging rates and assemblages throughout the year (Gomo et al., 2020; Ray et al., 2014). Likewise, competition for carrion resources is driven by predator-prey interaction patterns giving carrion removal within ecosystems additional variation (DeVault et al., 2004; Wilmers et al., 2003; Wilmers and Getz, 2004; Wilmers and Post, 2006). While abiotic and biotic factors affecting carcass persistence are well documented, few have simultaneously addressed both. This becomes increasingly important with scavenging in temperate zones as animals follow seasonal patterns (Allen et al., 2014; Benbow et al., 2013) adding a layer of complexity as climate influences both assemblages of scavengers and decay rate.

In an Australian context, temperate montane environments, such as in Kosciuszko National Park (NP), southern New South Wales, are home to several vertebrate scavengers: endemic (brush-tail possums: *Trichosurus vulpecula*, corvids: *Corvidae spp.*, dingos: *Canis dingo*, eastern quolls: *Dasyurus viverrinus*, wedge-tail eagles: *Aquila audax*) and exotic (cats: *Felis catus*, foxes: *Vulpes vulpes*, pigs: *Sus scrofa*); as well as invertebrate scavengers: endemic (blow flies: *Calliphoridae*, beetles: *Staphylinidae*, *Silphidae*, *Scarabaeidae*, ants: *Formicidae*) and exotic (European wasps: *Vespidae*). Carrion input from large mammals comes from endemic macropods (*Macropodidae*) as well as exotic ungulates (feral horses, *Equus caballus*, and deer *Cervidae spp.*) (New South Wales et al., 2006; Ward-Jones et al., 2019). Understanding the seasonal patterns of scavenging regimes in Kosciuszko NP will give insight about whether the local scavenging assemblage has the functional capacity to remove carcasses from the environment.

In this study, I examined the functional roles of vertebrate and insect scavenger guilds in Kosciuszko NP and their contributions to carrion decomposition by testing the following hypotheses:

1) Carcass persistence will be greatest in the colder seasons of autumn and winter. This is because lower temperatures will suppress decomposition rates and scavenger activity.
2) Carcass persistence will be greatest with vertebrate and insect exclusion followed by vertebrate only exclusion, then no exclusion. This is because insect and vertebrate scavengers have complementary functional roles and their combined presence at carcasses will have the greatest effect on decomposition.

To test these hypotheses, I monitored kangaroo carcasses across four seasons and under scavenger exclusion scenarios. The results provide insights into the current state and functional roles of Kosciuszko NP's scavenger guild. I intend for this research to help ecologists and managers understand how the scavenger communities or carcass loads might be managed to benefit Kosciuszko NP's delicate ecosystem.

Materials and Methods

Study Site

This study was conducted in Kosciuszko NP in the Australian alpine and subalpine ecotones centred around 148.489 -36.30346 and between the altitudes of 1074m and 1556m (Figure 12). The forest is dominated by gum trees (*Eucalyptus spp.*) with a moderate woody understory (Figure 13). The groundcover consisted primarily of bark from the surrounding Eucalypt spp. with occasional small forbs and grasses. The nearest Bureau of Meteorology station to the study transect is Hotel Kosciuszko which records an annual mean range of 3.7°C to 18.7°C with mean precipitation of 1,275.4mm (Bureau of Meteorology, 2020). Temperature was also recorded on each site's remote cameras which ranged from -8°C to 43°C. Typical annual snowfall occurs between June through October. Significant snowfall was recorded at the study sites in the winter and spring treatments. The study area was not impacted by the summer 2019-2020 wildfires although smoke and ash were recorded by a single camera from a remote fire. During the study there were several feral animal removal efforts targeting deer, pigs, and canids conducted by New South Wales National Parks and Wildlife Service. Kosciuszko NP is an ideal comparative analogue to temperate montane environments rigorously studied in the northern hemisphere (Independent Scientific Committee (N.S.W.), 2003).

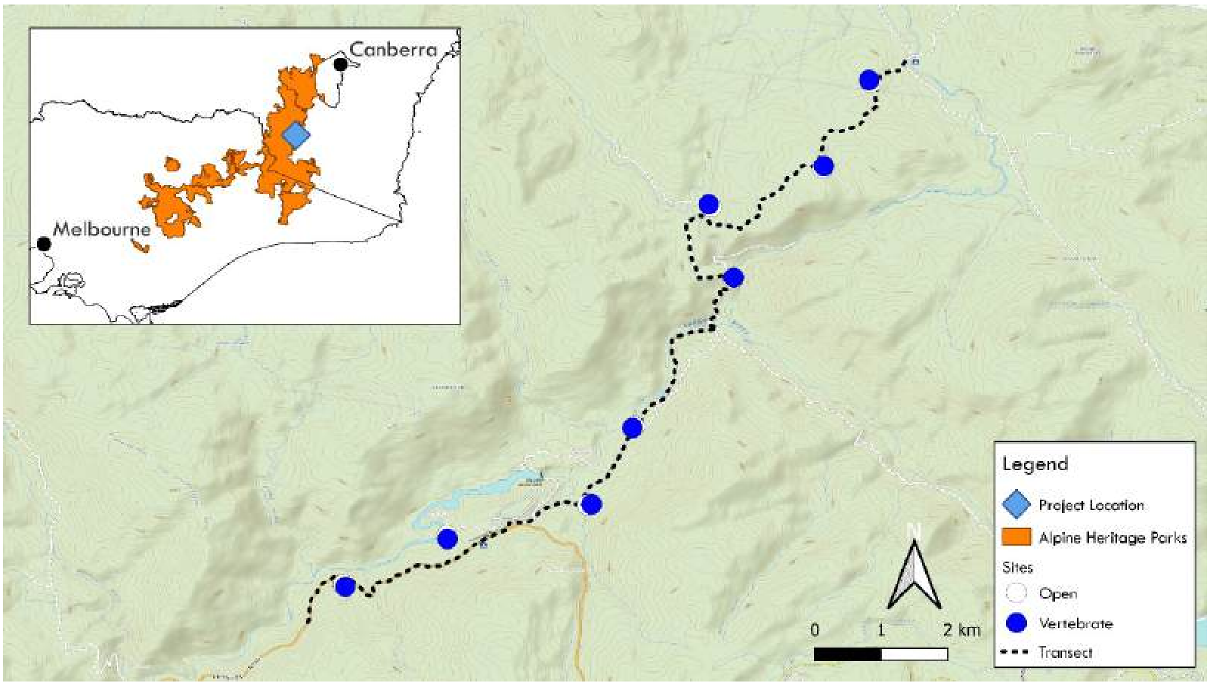


Figure 12. An overview of the study transect and the exclusionary treatment sites in Kosciuszko National Park. The study transect originates in the Botherum plains to the north-east and follows Island Bend Fire Trail. It terminates on Guthega Road in the south-west. The Park is in the Australian alpine region which span across southern New South Wales and eastern Victoria between Canberra and Melbourne. Kosciuszko NP occupies most of the alpine region in New South Wales.

Figure 13. Seasons and canopy cover at Kosciuszko National Park. A) Hardwood forest in autumn, March. B) Hardwood forest in winter, July.

Field Methods

I deployed 88 eastern grey kangaroo (*Macropus giganteus*) carcasses between March 2020 and April 2021 across four distinct seasons. Carcasses were sourced adjacent to Kosciuszko NP from agricultural pest animal culls and from licensed harvesters following New South Wales collection guidelines outlined in our scientific license (SL102334). Carcasses were presented intact with exception of entry and exit wounds from firearm ordinance during collection. We deployed carcasses in eucalypt forests with similar canopy cover along a single transect. A visual and photographic comparison of canopy cover and slope was used to standardise habitat between placements. The transect was chosen within the park boundaries following the length and curves of Island Bend Fire Trail, an un-interrupted forest area with minimal human impact. Carcass sites were not re-used between seasons to avoid habituation and pseudo-replication. Instead, new study sites were established and offset by 2 kilometres from the previous deployment and no closer than 500 metres from preceding deployments older than 6 months.

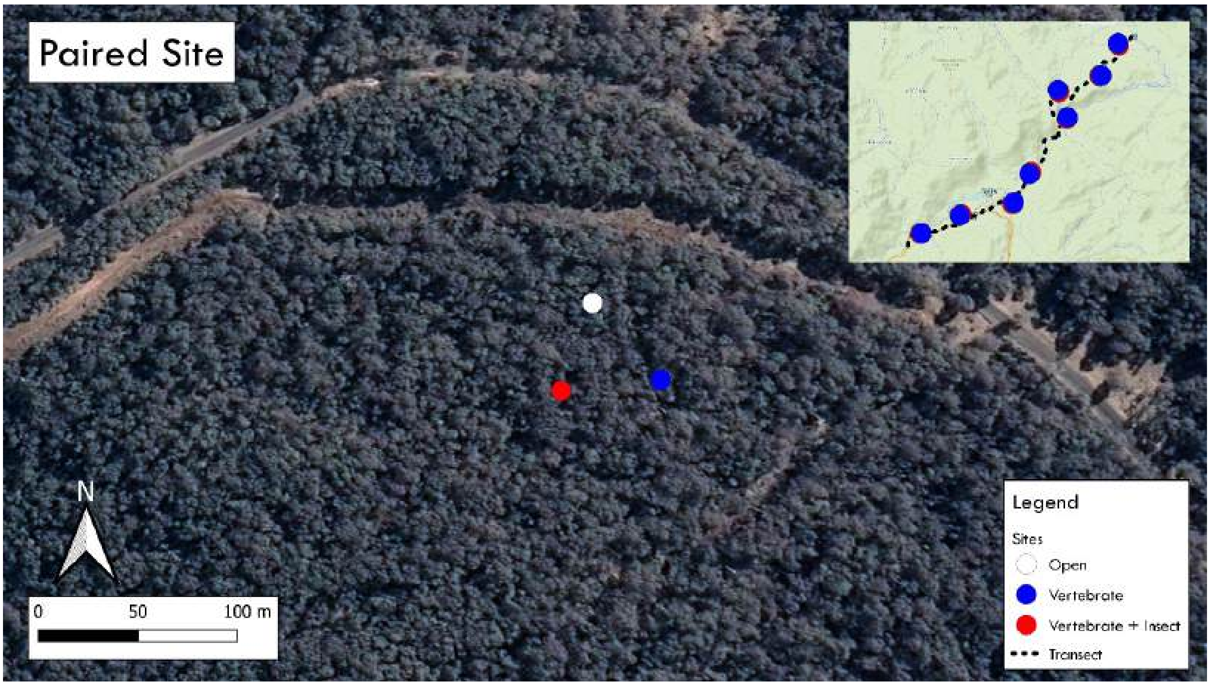


Figure 14: A paired site along the experimental transect in Kosciuszko NP showing the scavenger guild exclusionary gradient. The markers in order of decreasing access by scavengers are open / no exclusion (white), vertebrate exclusion (blue) and vertebrate + insect exclusion (red). Each site on the transect contains all three treatments.

Eight sites were established during autumn (March 2020), winter (July 2020), spring (September 2020), and summer (January 2021). Each site consisting of three carcass treatments: open (no exclusion), caged (vertebrate exclusion), and caged with insect mesh (vertebrate + insect exclusion). The winter replicate lacked a vertebrate + insect exclusion treatment due to the extreme inactivity of insects during cold. Seasonal replicates were monitored for 100 days or until majority had reached 10% biomass remaining. Open sites were placed no less than 100 metres from the road with paired caged sites 50 metres from each other carcass (Figure 14). Caged sites had a steel mesh walls (5cm aperture, 2.5mm gauge) and chicken wire (5cm aperture, 1mm gauge) with cubic dimensions (2 × 1 × 1 metres). The insect suppression cages had additional aluminium insect meshing (1mm gauge) secured flush to the walls and suspended above the carcass on the ceiling (Figure 15). Carcass body condition, sex, and weight were recorded upon deployment.

Figure 15. A depiction of carcasses deployed at each paired sites for the scavenger guild exclusion gradient. In order of decreasing access by scavenger guild: A) open / no exclusion, carcass is secured to ground, B) vertebrate exclusion, carcass is secured inside the cage, and C) vertebrate + insect exclusion, carcass is secured inside the cage and lined with fly-screen mesh.

To quantify carcass decay rates and vertebrate scavenger activity, each carcass was monitored with a Reconyx PC800 Hyperfire™ camera either three meters distance on a star picket (open sites) or as far as possible on a cage wall (caged sites). Time lapse imagery was used to estimate carcass biomass loss-rate and times at which decomposition stages were reached. Time lapses at caged sites were taken at a rate of 1 photo every 15 minutes continuously to get fine detail of decomposition and invertebrate colonisation. Open sites collected time lapse imagery daily at 10:00 and 14:00 only due to power and storage constraints with collecting motion triggered images. Where possible, additional cameras (equipment limited) were placed on open sites collecting time lapse imagery with cage site settings (approximately four open sites per replicate).

Decay rate and decomposition stage were estimated from time lapse imagery. To mediate bias of precise mass estimates attained from imagery, measurements of biomass were split into the following six categories: “0-10%”, “11-29%”, “30-49%”, “50-69%”, “70-89%”, “90-99%”. Decomposition stages were determined using criteria outlined by Carter et al. (2007) and Payne (1965) and labelled as “fresh”, “early/bloat”, “active”, “advanced”, and “dry”.

Vertebrate scavenger activity on open carcasses was assessed from motion-triggered sequences (10-photo burst, rapid-fire, no delay). Image sequences were tagged with the individual species visible in the frame and if the animal was feeding (visibly consuming the carcass or implied from their movements). Vertebrate feeding events were defined as the number of images that were tagged with feeding behaviour. To ensure maximum visibility of vertebrate behaviour at open sites, carcasses were secured to the ground using two star-pickets (60cm) and tie-wire. Camera function at open and caged sites was checked every three days, and photographs were collected on completion of each replicate.

Insects were collected in two 120ml pitfall traps on open and vertebrate exclusion sites for the first 72 hours of carcass monitoring. Pitfall traps were placed 20cm from the head and base of tail and filled half-way with ethylene glycol as a preservative (Barton and Evans, 2017; Spencer et al., 2020). Insects were counted, then sorted into broad taxonomic groups: ants (Formicidae), beetles (Coleoptera), flies (Diptera), and wasps (Vespidae) by myself and a honours student at the University of Sydney. These taxa were chosen because of their high abundance in collected pitfall traps and their known interactions with carrion. Insects were identified with an Olympus stereo microscope SZ40 model (0.67X to 5X) microscope using online reference tool "What bug is that?" (CSIRO, 2012).

To assess the effectiveness of the insect exclusion effect, sticky glue-traps were placed on the inside and outside of the vertebrate and insect exclusion cages upon carcass deployment then photographed after 72-hours. All insects appearing on the glue-traps were then tallied. Pitfall traps were not deployed at vertebrate + insect exclusion sites to avoid compromising the mesh integrity during collection. The total exclusion of insects is difficult to obtain, but the sticky traps deployed showed significantly more insects were trapped in the vertebrate exclusion cages (without mesh) than the vertebrate + insect exclusion cages (meshed) (Appendix 4) suggesting that this treatment provided a delayed insect response or a suppression effect rather than complete exclusion (Pechal et al., 2014).

Carcass Persistence

Carcass persistence for each treatment was modelled using Cox proportional hazards regression. Model parameters were the number of days until 10% biomass was attained or the end of the monitoring period with a status of progressing through to that stage or not reaching it. Statistical analysis was performed using Program R version 4.0 and greater (R Core Team, 2020). Cox proportional hazards (Cox) models were fit to the data using packages `survival` (3.2.11) (Therneau and Grambsch, 2000) and `survminer` (0.4.9) (Kassambara et al., 2021) to model the regression of carcass survival time until 10% biomass reached. Kaplan-Meier survival curves using the same packages were fit to the data for a visual representation of the Cox models and logrank tests were performed to assess differences between survival of carcasses between seasons and treatments. Variables used in the Cox model were tested for temporal independence. Categorical biomass of 10% was established and used because it is synonymous with reaching dry decay. Carcasses did not completely disintegrate during each monitoring season, however, the removal of biomass down to 10% signifies a functional change of resources provided by the carcass as the vast majority of nutrients contained in the soft tissues have been consumed leaving hardier bones and sinew that take much longer to decompose (Carter et al., 2007).

To assess differences between seasons, a Cox proportional hazards model of all replicates and treatments was fitted to attain seasonal patterns in decay rate. This was examined further in a pairwise comparison of p-values to assess relative decay rates within and across seasons and treatments. Pairwise comparison values were adjusted for comparison using methods described by Holm (1979).

Seasonal treatments were then grouped into warm (spring, summer) and cold (autumn, winter) and were modelled with carcasses reaching 10% and 50% biomass markers respectively. This was done because decay had a high correlation with temperature and thus carcasses in colder seasonal replicates did not decay to 10% biomass in high enough numbers to analyse. Instead, a 50% biomass marker was chosen for carcass decay in colder seasons as it represents significant biomass loss and a trajectory towards disintegration.

Results

From March 2020 through April 2021, 88 carcasses (2,425kg) were monitored across the four seasons for a total of 391 days. Photos taken by remote cameras totalled 939,636 with 48% containing vertebrate feeding events. At open sites, there were 454,701 photos of vertebrates feeding on carcasses (feeding activity), 41.6% of which were corvids and 27.3% were brush-tailed possums (Figure 16A). Spring has the most vertebrate scavenging activity (33%), followed by winter (30%), autumn (26%), and summer (11%). Insects collected in pitfall traps and counted totalled 8,248. Insect activity observed during sampling was skewed to autumn and summer when temperatures were warmer. Ants comprised most insects appearing in the first 72 hours (Figure 16B). Mean carcass persistence in days to 10% biomass was 38.6 (se = 18.7) ranging from 10 to 78 (Appendix 11); however, 44 carcasses were omitted in determining mean carcass persistence because they did not decay to 10% biomass. Carcass persistence was much longer in the colder seasons of autumn and winter with the majority of carcasses monitored during these seasons not decaying to less than 10% biomass or reaching the dry decay stage.

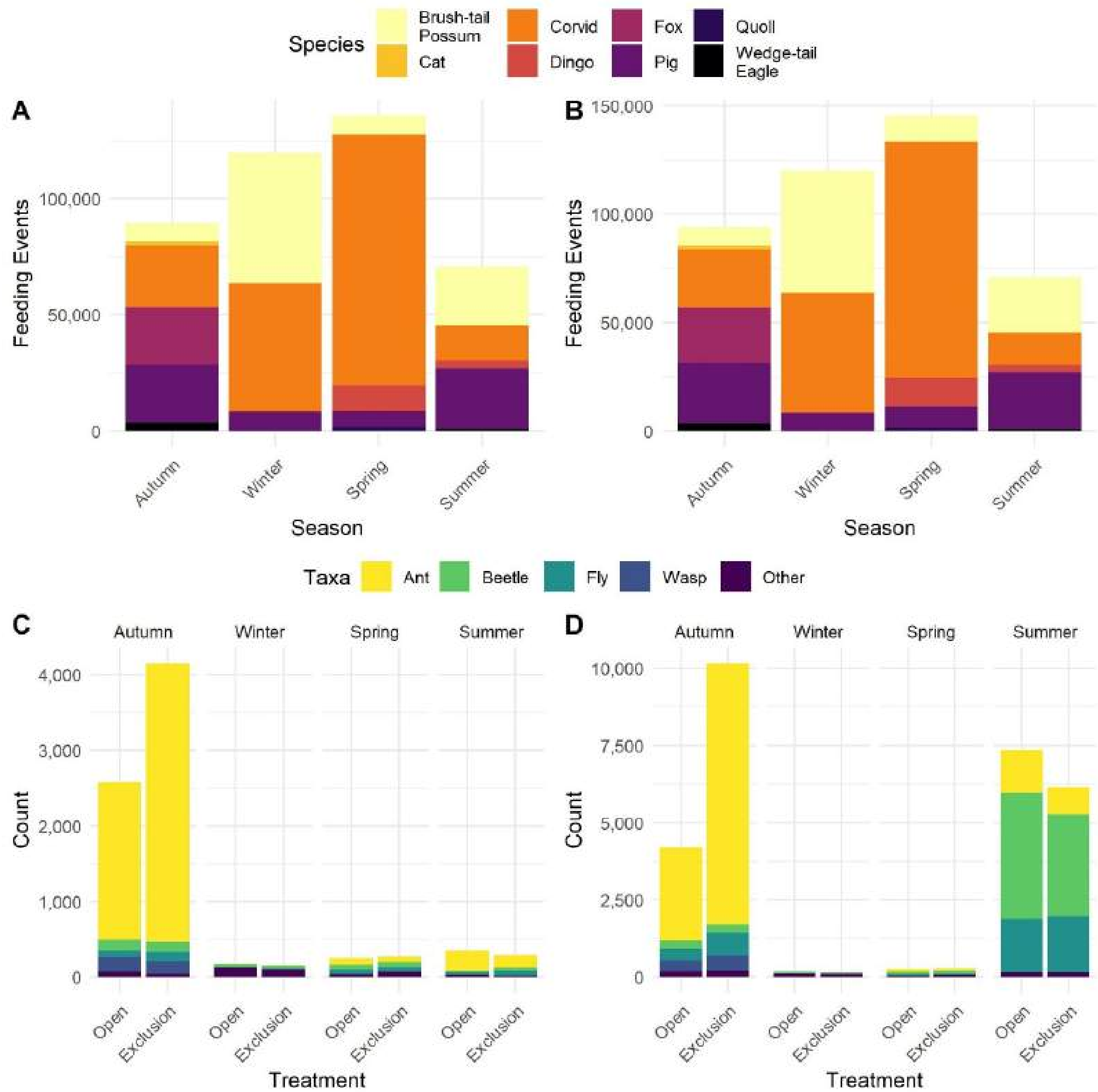


Figure 16: Vertebrate (A, B) and insect (C, D) scavenger community assemblages with standardised collection (A, C) and in total (B, D). Vertebrate feeding activity was tallied at each open site and insects were sampled from open and vertebrate exclusion sites. The charts are A) vertebrate feeding activity standardised for the minimum monitoring period of 78 days (summer replicate), B) total vertebrate feeding activity for each seasonal replicate, C) insect abundance for the first three days of carcass decomposition, and D) total insect abundance for all seasonal replicates. The comparison between C and D highlights the number of insects that appeared in the summer replicate despite the low abundance during the first collection period (days 0-3). Low temperatures and precipitation during the first summer insect collection may have slowed or deterred colonisation (Appendix 2; Appendix 30). For a comprehensive description of the insect sampling complications, see Appendix 12. Vertebrate activity between the standardised (A) and total (B) is similar.

Modelling Annual Decomposition Trends

Seasonal trends had a far greater effect on carcass persistence than experimental effects (Table 1; Table 2; Figure 17). As indicated by the regression coefficient and hazard ratio, carcass persistence was longest in winter followed by autumn, spring, then summer (Table 1). Autumn and winter replicates (cold seasons) did not vary from one another; likewise, spring and summer (warm seasons) had little variation with notable exception of the summer control (open) treatment (Table 2). However, there was significant variation between cold seasons and warm season replicates (Table 2). Winter exhibited little variation because of the lack of carcasses during that replicate that made it to 10% biomass within the allotted monitoring period. The mean ratio of effects size of season to experimental treatment was 184:1 (Table 1) creating a difficulty in modelling annual persistence with the treatments in a singular model thus separate Cox proportional hazard models were fit to the replicates to compare trends.

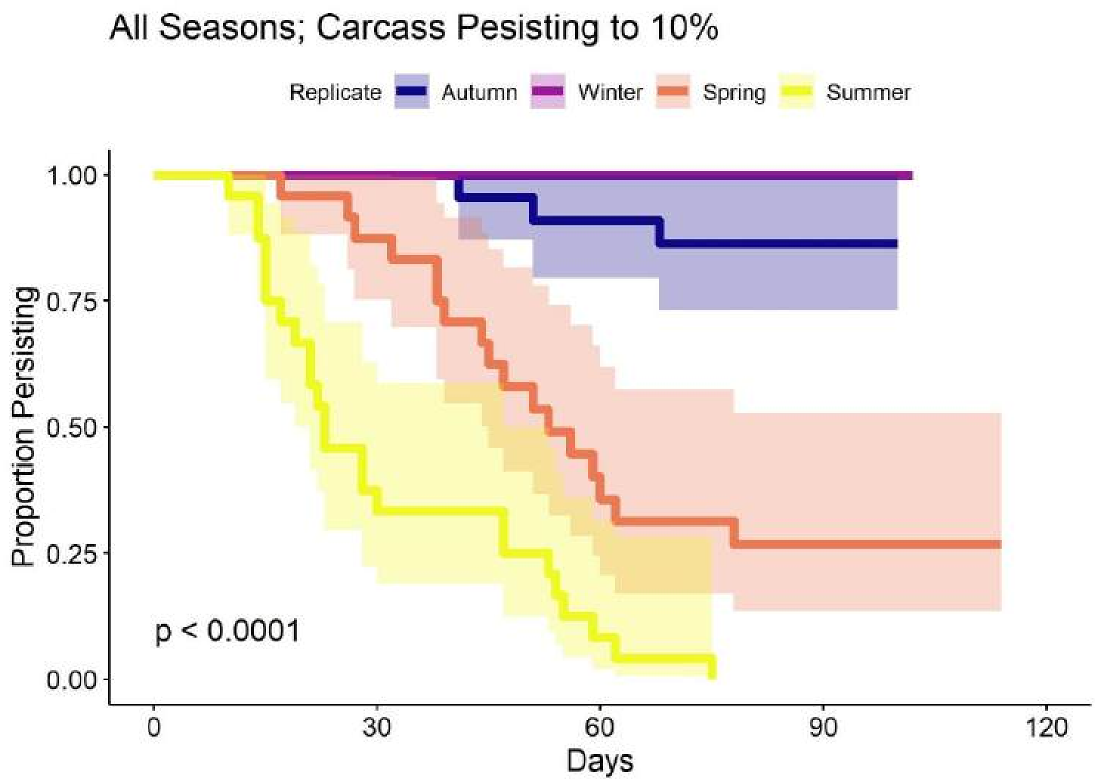


Figure 17: Kaplan-Meier survival curve of carcass persistence to 10% biomass across seasonal replicates (λ_{RT} = 75.24 on 3 df; $p << 0.05$). As indicated by the overall logrank p-value ($p < 0.0001$) there are significant differences between the survival curves. Differences between seasons and treatments are examined in Table 2.

Table 1: Coefficients and confidence intervals for Cox proportional hazard model of carcass persistence to 10% biomass with seasonal and experimental factors.

Factor		$\beta_{regression}$	se_{β}	z	p	$e^{\beta}_{hazard\ ratio}$	$CI_{95\%}$
Season	Winter	-17.968	4834.451	-0.004	0.997	1.6E-08	0 - Inf
	Spring	2.661	0.650	4.096	4.2E-05	14.314	4.007 - 51.138
	Summer	4.287	0.692	6.199	5.7E-10	72.771	18.761 - 282.267
Treatment	Vertebrate	-1.639	0.413	-3.971	7.1E-05	0.194	0.086 - 0.436
	Insect	-2.135	0.438	-4.872	1.1E-06	0.118	0.050 - 0.279

Table 2: Pairwise comparison of logrank p-values from the Cox proportional hazards model of season and treatment on carcass persistence to 10% biomass. P-values were adjusted for comparison using methods described by Holm (1979).

Pairwise comparison of logrank values from survival models to 10% biomass

		Autumn			Winter		Spring			Summer	
		Open	Vert	Insect	Open	Vert	Open	Vert	Insect	Open	Vert
Autumn	Vert										
	Insect										
Winter	Open										
	Vert										
Spring	Open	*	*	*	*	*					
	Vert		*	*	*	*					
	Insect										
Summer	Open	*	*	*	*	*	*	*	*		
	Vert		*	*	*	*					
	Insect	.	*	*	*	*			.	*	

* = p < 0.05; . = p < 0.1

Table 3: Coefficients and confidence intervals for Cox proportional hazards models of carcass persistence within each season with experimental factors. Cold seasons (autumn and winter) to 50% biomass and warm seasons (spring and summer) to 10% biomass. Seasonal models were analysed separately, and p-values have not been adjusted for comparison across replicates.

Season	Biomass	Treatment	$\beta_{regression}$	se_β	z	p	$e^{\beta}_{hazard\ ratio}$	$CI_{95\%}$
Autumn	50%	Cage	-0.606	0.674	-0.899	0.369	0.546	0.146 - 2.045
		Cage + Mesh	-1.982	1.097	-1.806	0.071	0.138	0.016 - 1.184
Winter	50%	Cage	0.549	0.841	0.653	0.514	1.731	0.333 - 8.992
		Cage + Mesh	-	-	-	-	-	-
Spring	10%	Cage	-0.739	0.533	-1.386	0.166	0.478	0.168 - 1.358
		Cage + Mesh	-2.541	0.848	-2.995	0.003	0.079	0.015 - 0.416
Summer	10%	Cage	-1.839	0.624	-2.947	0.003	0.159	0.047 - 0.540
		Cage + Mesh	-1.800	0.598	-3.007	0.003	0.165	0.051 - 0.534

Carcass persistence in cold seasons

In colder seasons, autumn and winter, biomass deteriorated significantly slower than in warmer seasons, spring, and summer. Indeed, only 3 carcasses from autumn and winter reached 10% biomass after 100 days of monitoring (Appendix 1). To assess carcass decomposition during colder seasons we instead analysed the half-life of its mass (days until carcass reaches 50% biomass) as 15 of the carcasses reached that marker. For both autumn (λ_{RT}=4.61 on 2 df, p=0.1) and winter (λ_{RT}=0.46 on 1 df, p=0.5) there were no significant differences between replicates (Table 2) and between any experimental treatments (Table 4). Both autumn and winter exhibited high errors ($\beta < |se_\beta|$) and wide confidence intervals furthering a similarity between treatments (Table 3; Figure 18).

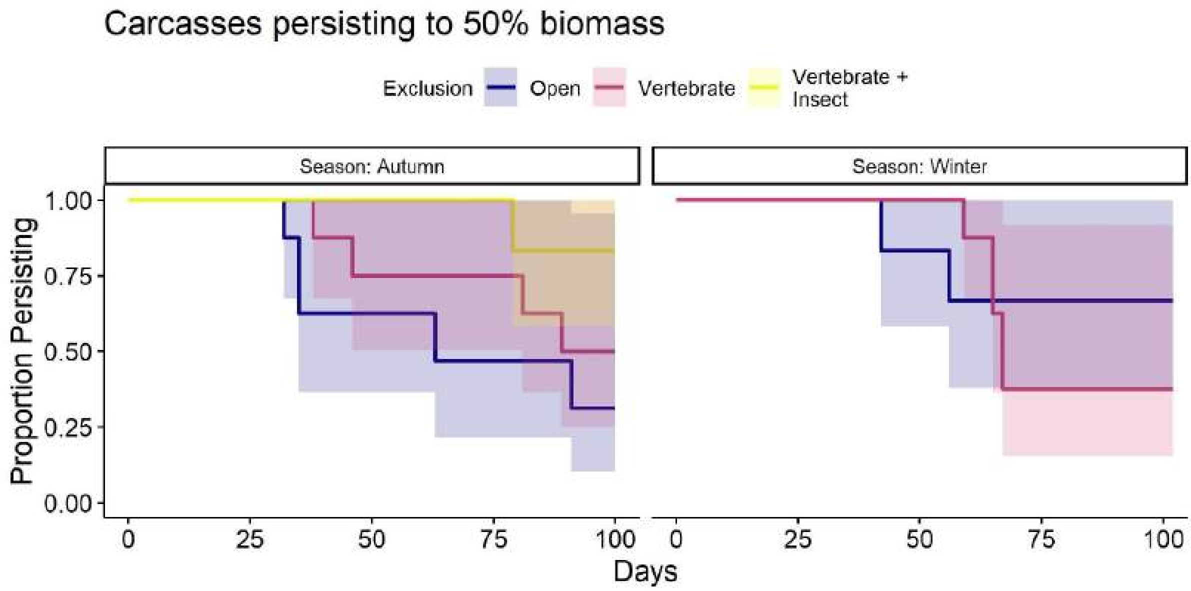


Figure 18: Kaplan-Meier survival curves of carcasses in autumn and winter persisting to 50% biomass with exclusion treatments.

Carcass persistence in warm seasons

In contrast to the colder seasons, spring and summer replicates exhibited much shorter carcass persistence (Figure 16), and the majority decomposed to 10% biomass within the monitoring periods (Appendix 1). There were few significant differences with treatments with exception for the summer control (open) sites (Table 2). However, within each treatment there are differing decomposition schemes: all three treatments in spring decayed at a similar rate while in summer the open treatment decayed more quickly than both caged treatments.

The spring replicate exhibited greater carcass persistence as carcasses were deployed in colder climate and snow fall but quickly dissipated as season progressed towards warmer temperatures (Appendix 2). A Cox proportional hazards model of this replicate was an adequate fit (λ_{RT}=12.52 on 2 df, p=0.002) and showed significantly greater carcass persistence with the insect exclusion treatment (Table 3; Table 4). The treatment's effect showed greatest regression with open, followed by vertebrate exclusion, then insect suppression but its effect size was small (Table 3).

Similar to spring, the summer replicate shows short carcass persistence but has slightly different treatment effects. A Cox proportional hazards model on this replicate was an adequate fit (λ_{RT}=10.28 on 2 df, p=0.006). In a pairwise comparison of the model, the vertebrate exclusion and insect suppression sites shows differences to the open sites (Table 4). Further analysis into this model's covariates and confidence intervals revealed that carcass persistence is shortest with the open sites and greatest with the caged sites; and both cage treatments appear identical (Table 3; Figure 19). Although there is a clear distinction between the open and caged survival curves (Figure 19), the effect size is relatively low as indicated by the hazard ratios (Table 1). These small effect sizes and indeed carcass persistence are the result and actions from the scavenging assemblages that visit.

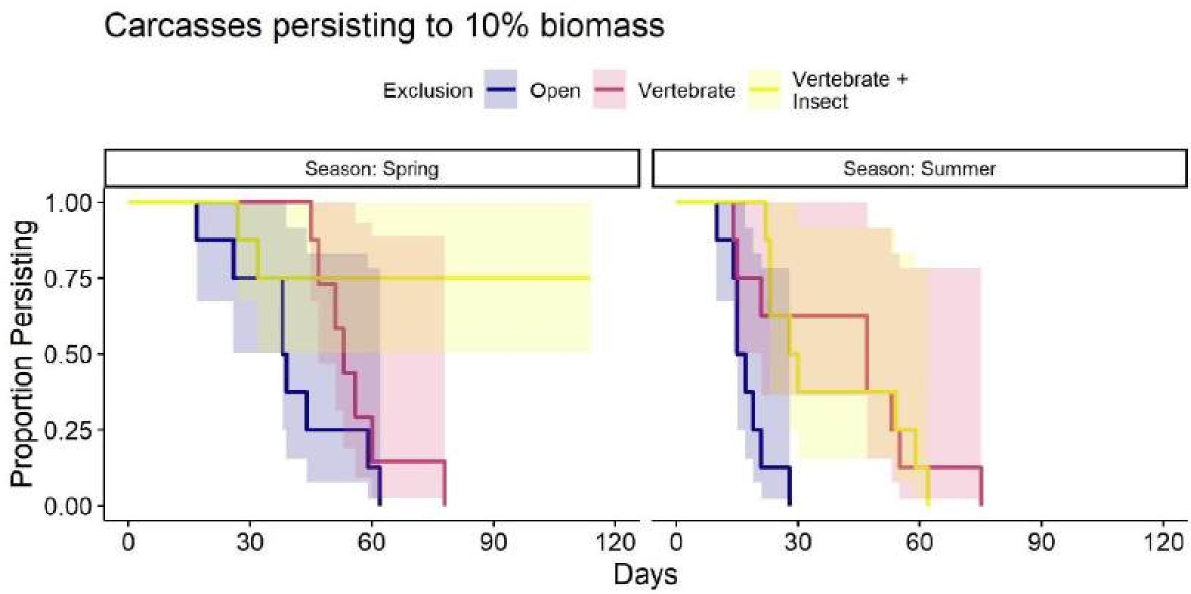


Figure 19: Kaplan-Meier survival curves of carcasses in spring and summer persisting to 10% biomass with exclusion treatments.

Table 4. A grid of four Cox proportional hazard models of each seasonal replicate with pairwise comparisons of logrank p-values within seasons. Models were fit to each replicate separately with the event markers of 50% biomass for cold seasons (autumn and winter) and 10% biomass for warm seasons (spring and summer).

Pairwise p-value table of Cox Proportional Hazards Model within Seasons

50% Biomass — Autumn

	Open	Vertebrate
Vertebrate	0.409	
Vertebrate + Insect	0.115	0.409

50% Biomass — Winter

	Open	Vertebrate
Vertebrate	0.540	
Vertebrate + Insect	-	-

10% Biomass — Spring

	Open	Vertebrate
Vertebrate	0.116	
Vertebrate + Insect	0.021	0.039

10% Biomass — Summer

	Open	Vertebrate
Vertebrate	0.024	
Vertebrate + Insect	0.003	0.936

Discussion

In many ecosystems, scavenging carrion provides an abundant and universally accessible nutrient source, which can be acquired with less energy expended compared to predation (Wilson and Wolkovich, 2011). But nutrient recycling from carrion is subject to abiotic and biotic patterns that affect scavenging rates and carcass availability. Disturbances that affect scavenger species may also result in a loss of ecosystem function prolonging carrion persistence (Huijbers et al., 2015). Similar to other temperate montane ecosystems, Kosciuszko NP's vertebrate and insect scavenger populations follow seasonal patterns which influence the ability of scavengers to process carrion. In this study, I demonstrate 1) that decay rates are longer in colder seasons, 2) the vertebrate scavenging guild has a limited capacity to remove carrion during colder seasons, which reflects limited redundancy in the absence of insect scavengers, 3) insect scavenging during warmer months leads to a decrease in carcass persistence, especially in later stages of decomposition. This suggests there is a narrow window where carcasses are consumed efficiently; only during the warmer months when insects are at their "peak".

In line with hypothesis 1, carcasses deployed in colder months took longer to decay than in warmer seasons (Figure 17). Indeed, the majority of carcasses deployed in autumn and winter did not fully decompose, even after 100 days and may have continued to persist until temperatures warmed (Appendix 1). This was despite the largest amount of vertebrate scavenging activity on carcasses occurring during the colder season (Figure 16A; Appendix 5); a pattern that has been found in other studies (DeVault et al., 2004; Turner et al., 2020). This was most likely caused by colder temperatures suppressing insect and microbial activity allowing for longer availability of nutrients to vertebrates (Peers et al., 2020; Turner et al., 2017). During the sequestration of insects and microbes, vertebrates would then assume more of a role in the removal of carcass biomass. This suggests a small capacity of redundant function between these scavenger guilds to remove carrion as vertebrates were able to partially consume carcasses while insects were suppressed.

However, in cold seasons vertebrate scavenging did not remove carcass biomass in significant quantities to impact carcass persistence (Figure 18, Table 4). In temperate ecosystems, scavenging by vertebrates tends to increase with colder temperatures leading to a higher consumption of carrion (DeVault et al., 2004). In this study, vertebrates did not exert a functional contribution to remove large mammalian carcasses suggesting some ecosystem dysfunction (Newsome et al., 2021). Therefore, carcass persistence in winter among open sites may potentially be explained by the following scenarios: 1) vertebrates do not contribute to carrion removal in a significant way, 2) the vertebrate scavenger assemblage is dominated by mesoscavengers who have limited capacity to remove carcass biomass quickly , 3) there is an overabundance of carrion, or 4) vertebrates were unable to locate carcasses efficiently (Table 5). From the assemblage of vertebrate scavengers in winter, the predominate species were corvids and brush-tailed possums, possibly highlighting a lack of community structure as apex predators such as the dingo (Olson et al., 2012; Wilson and Wolkovich, 2011). In similar ecosystems, scavenging on large carcasses from intact vertebrate scavenging guilds tends to be dominated and structured around apex predators (Moleón et al., 2015; Olson et al., 2012).

In contrast, vertebrate scavenging did influence carcass persistence in summer, especially towards the end of decomposition (Figure 20). This was despite vertebrate scavenging rates being relatively low, suggesting additive scavenging effects amongst the insect and vertebrate guilds as their combined contributions to carcass removal ultimately showed the shortest carcass persistence compared to the exclusion cages (Figure 19). In summer, open carcasses persisted 17.4 (±5.4) days while caged persisted 40.9 (±22.0) days. These caged carcasses were 84% (46-95%) more likely to survive 1.8 times longer than exposed carcasses (Table 3). This suggests a complimentary function between these scavenging guilds as vertebrates may facilitate insect consumption of biomass by fragmenting the carcass and facilitating carcass biomass access. Vertebrate's effect of accelerating decay most likely came from their ability to remove large and heavy fragments of carcass (such as bones) that insects can't efficiently process. This may be evidenced by the time-lapse imagery as decay recorded by the cameras progressed similarly across treatments during active decomposition. At the conclusion of the summer replicate, open carcasses showed many remains scattered beyond the initial resting site by means of vertebrate action.

Autumn and spring replicates showed transitions from and to insect-driven decomposition as carcasses were deployed and temperatures rapidly changed. The autumn treatment was deployed at the beginning of the season while temperatures were still warm (Appendix 2). Temperatures then quickly cooled, subduing insect activity and thus prolonging the decay (Figure 18). In contrast, the spring treatment was deployed during cold/snowy weather, but the climate quickly warmed ending insect dormancy allowing them to scavenge leading to an increase in the decay rate (Figure 19). This is corroborated by the mean consumption of carrion biomass between seasons as winter and autumn held the least amount of biomass change at the end of the replicate while spring and summer were almost entirely consumed (Appendix 7). This suggests a peak of scavenging efficiency with warm temperatures in late spring through summer.

Decay within the insect exclusion treatment most resembled the vertebrate exclusion treatment. There was a slight suppression effect from the insect mesh that was most noticeable in autumn when insects were not as active (Figure 18). Unfortunately, in spring and summer, the time lapse imagery showed insects were able to penetrate the insect mesh and colonise carcasses after the first few days of deployment. This created a delay of access to the carcass rather than a complete or partial exclusion as evidenced by the sticky traps deployed during the first three days or monitoring (Appendix 4). This gradient of exclusion was intended to isolate the contributions to decomposition from each added scavenger guilds but failed at the insect exclusion during warm seasons as insects during that time were tenacious in their attack. Despite insect access, there was some evidence for a gradient of decay rates among all three exclusion treatments during autumn. During autumn when temperatures dropped (partially suppressing insect activity), the insect exclusion appeared to have been successful. Then, carcass persistence was its highest in the vertebrates/insect exclusion followed by the vertebrate exclusion, then exposed treatments (Figure 18). Thus, conclusions for the insect exclusion treatment are most robust with the autumn dataset. This conforms with other studies: the absence of insects prolongs carcass persistence (Payne, 1965; Pechal et al., 2014).

This study demonstrated Kosciuszko NP's narrow capacity to efficiently recycle carrion. Both vertebrate and insect scavengers act on carcasses in different ways that produced an additive effect when temperatures are at their highest. However, this dynamic changes as temperatures fall and vertebrates express a limited redundancy to remove carrion biomass. The effective result is carrion is only fully consumed when temperatures are warm, and insects are at their most active (Figure 20). This is important in managing large feral mammal populations as culling efforts to reduce large feral mammals will inevitably produce carrion surges, but the biomass will only be recycled efficiently during late spring to summer. Additionally, further research to quantify Kosciuszko NP's necrobiome should be conducted to better understand its dysfunctional vertebrate scavenger guild. In the meantime, I propose avoiding disruptions to Kosciusko NP's necrobiome by favouring feral mammal management during periods of peak scavenging efficiency: spring and summer.

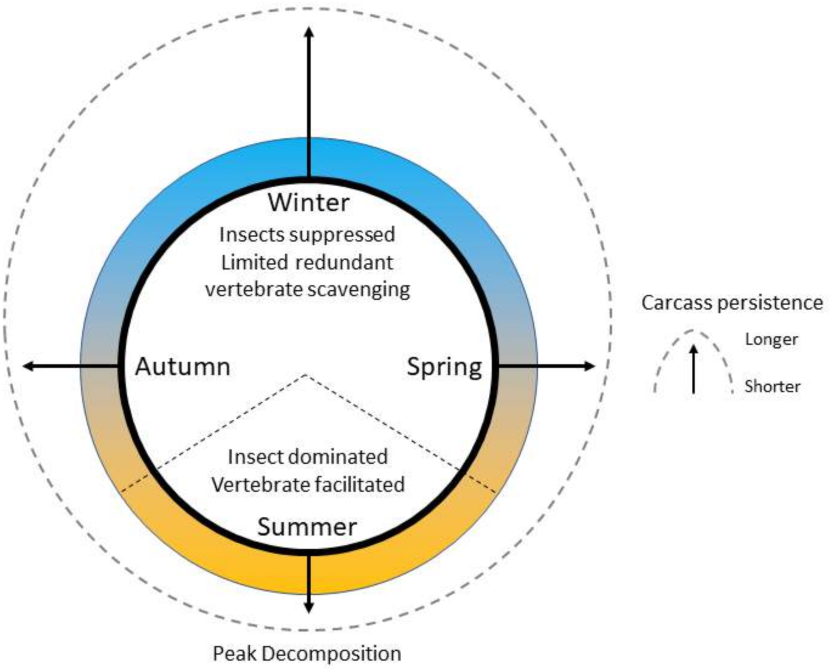


Figure 20: A conceptual scavenging regime of Kosciuszko National Park showing annual trends of carcass persistence. Carrion in warmer seasons (indicated in orange) are dominated by insect scavengers and are facilitated by facultative vertebrate scavengers. Colder seasons (blue) have suppressed insects, lowering their competition with vertebrates but consequently increasing carcass persistence due to dysfunction in ecosystem function. Carrion is only processed efficiently during "peak decomposition" in warmer seasons when insects are at their most active.

References

Allen, M., Elbroch, L., Casady, D., Wittmer, H., 2014. Seasonal variation in the feeding ecology of pumas (Puma concolor) in northern California. Canadian Journal of Zoology 92, 397–403. https://doi.org/10.1139/cjz-2013-0284

Barton, P.S., Cunningham, S.A., Lindenmayer, D.B., Manning, A.D., 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia 171, 761–772. https://doi.org/10.1007/s00442-012-2460-3

Barton, P.S., Evans, M.J., 2017. Insect biodiversity meets ecosystem function: differential effects of habitat and insects on carrion decomposition. Ecological Entomology 42, 364–374. https://doi.org/10.1111/een.12395

Beasley, J.C., Olson, Z.H., Devault, T.L., 2012. Carrion cycling in food webs: Comparisons among terrestrial and marine ecosystems. Oikos 121, 1021–1026. https://doi.org/10.1111/j.1600-0706.2012.20353.x

Benbow, M., Lewis, A., Tomberlin, J., Pechal, J., 2013. Seasonal Necrophagous Insect Community Assembly During Vertebrate Carrion Decomposition. Journal of Medical Entomology 50, 440–450. https://doi.org/10.1603/ME12194

Benbow, M.E., Tomberlin, J.K., Tarone, A.M. (Eds.), 2015. Carrion Ecology, Evolution, and Their Applications. CRC Press, Boca Raton. https://doi.org/10.1201/b18819

Biggs, C.R., Yeager, L.A., Bolser, D.G., Bonsell, C., Dichiera, A.M., Hou, Z., Keyser, S.R., Khursigara, A.J., Lu, K., Muth, A.F., Negrete, B., Erisman, B.E., 2020. Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. Ecosphere 11, e03184. https://doi.org/10.1002/ecs2.3184

Bureau of Meteorology, 2020. Summary statistics MOUNT KOSCIUSKO (HOTEL KOSCIUSKO) [WWW Document]. URL http://www.bom.gov.au/climate/averages/tables/cw_071012.shtml (accessed 11.4.20).

Cardinale, B., Srivastava, D., Duffy, J., Wright, J., Downing, A., Sankaran, M., Jouseau, C., 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443, 989–92. https://doi.org/10.1038/nature05202

Carter, D.O., Yellowlees, D., Tibbett, M., 2007. Cadaver decomposition in terrestrial ecosystems. Naturwissenschaften 94, 12–24. https://doi.org/10.1007/s00114-006-0159-1

CSIRO, 2012. What Bug Is That? The guide to Australian insect families. [WWW Document]. Taxonomy Research & Information Network. URL http://anic.ento.csiro.au/insectfamilies/ (accessed 10.18.21).

DeVault, T.L., Brisbin, Jr., I.L., Rhodes, Jr., O.E., 2004. Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers. Can. J. Zool. 82, 502–509. https://doi.org/10.1139/z04-022

Fonseca, C.R., Ganade, G., 2001. Species functional redundancy, random extinctions and the stability of ecosystems. Journal of Ecology 89, 118–125. https://doi.org/10.1046/j.1365-2745.2001.00528.x

Gomo, G., Rød-Eriksen, L., Andreassen, H.P., Mattisson, J., Odden, M., Devineau, O., Eide, N.E., 2020. Scavenger community structure along an environmental gradient from boreal forest to alpine tundra in Scandinavia. Ecology and Evolution 10, 12860–12869. https://doi.org/10.1002/ece3.6834

Holm, S., 1979. A Simple Sequentially Rejective Multiple Test Procedure. Scandinavian Journal of Statistics 6, 65–70.

Huijbers, C.M., Schlacher, T.A., Schoeman, D.S., Olds, A.D., Weston, M.A., Connolly, R.M., 2015. Limited functional redundancy in vertebrate scavenger guilds fails to compensate for the loss of raptors from urbanized sandy beaches. Diversity and Distributions 21, 55–63. https://doi.org/10.1111/ddi.12282

Independent Scientific Committee (N.S.W.), 2003. An assessment of the values of Kosciuszko National Park : interim report. National Parks and Wildlife Service, Queanbeyan NSW.

Kassambara, A., Kosinski, M., Biecek, P., 2021. survminer: Drawing Survival Curves using "ggplot2."

Moleón, M., Sánchez-Zapata, J.A., Sebastián-González, E., Owen-Smith, N., 2015. Carcass size shapes the structure and functioning of an African scavenging assemblage. Oikos 124, 1391–1403. https://doi.org/10.1111/oik.02222

Munoz-Lozano, C., Martin-Vega, D., Martinez-Carrasco, C., Sanchez-Zapata, J.A., Morales-Reyes, Z., Gonzalvez, M., Moleon, M., 2019. Avoidance of carnivore carcasses by vertebrate scavengers enables colonization by a diverse community of carrion insects. PLoS One 14, e0221890. https://doi.org/10.1371/journal.pone.0221890

New South Wales, Department of Environment and Conservation, Parks and Wildlife Division, New South Wales, Department of Environment and Conservation, 2006. Kosciuszko National Park plan of management: 2006. Dept. of Environment and Conservation NSW, Sydney South, N.S.W.

Newsome, T.M., Barton, B., Buck, J.C., DeBruyn, J., Spencer, E., Ripple, W.J., Barton, P.S., 2021. Monitoring the dead as an ecosystem indicator. Ecology and Evolution 11, 5844–5856. https://doi.org/10.1002/ece3.7542

O'Bryan, C.J., Braczkowski, A.R., Beyer, H.L., Carter, N.H., Watson, J.E.M., McDonald-Madden, E., 2018. The contribution of predators and scavengers to human well-being. Nat Ecol Evol 2, 229–236. https://doi.org/10.1038/s41559-017-0421-2

Ogada, D.L., Torchin, M.E., Kinnaird, M.F., Ezenwa, V.O., 2012. Effects of Vulture Declines on Facultative Scavengers and Potential Implications for Mammalian Disease Transmission: *Vulture Declines, Facultative Scavengers, and Disease Transmission*. Conservation Biology 26, 453–460. https://doi.org/10.1111/j.1523-1739.2012.01827.x

Olson, Z.H., Beasley, J.C., DeVault, T.L., Rhodes, O.E., 2012. Scavenger community response to the removal of a dominant scavenger. Oikos 121, 77–84. https://doi.org/10.1111/j.1600-0706.2011.19771.x

Payne, J.A., 1965. A Summer Carrion Study of the Baby Pig Sus Scrofa Linnaeus. Ecology 46, 592–602. https://doi.org/10.2307/1934999

Pechal, J.L., Benbow, M.E., Crippen, T.L., Tarone, A.M., Tomberlin, J.K., 2014. Delayed insect access alters carrion decomposition and necrophagous insect community assembly. ECOSPHERE 5. https://doi.org/10.1890/ES14-00022.1

Peers, M.J.L., Konkolics, S.M., Lamb, C.T., Majchrzak, Y.N., Menzies, A.K., Studd, E.K., Boonstra, R., Kenney, A.J., Krebs, C.J., Martinig, A.R., McCulloch, B., Silva, J., Garland, L., Boutin, S., 2020. Prey availability and ambient temperature influence carrion persistence in the boreal forest. Journal of Animal Ecology n/a. https://doi.org/10.1111/1365-2656.13275

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ray, R.-R., H. Seibold, M. Heurich, 2014. Invertebrates outcompete vertebrate facultative scavengers in simulated lynx kills in the Bavarian Forest National Park, Germany. Animal biodiversity and conservation 37.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and Ecological Effects of the World's Largest Carnivores. Science 343, 1241484–1241484. https://doi.org/10.1126/science.1241484

Rosenfeld, J.S., 2002. Functional redundancy in ecology and conservation. Oikos 98, 156–162. https://doi.org/10.1034/j.1600-0706.2002.980116.x

Sebastián-González, E., Barbosa, J.M., Pérez-García, J.M., Morales-Reyes, Z., Botella, F., Olea, P.P., Mateo-Tomás, P., Moleón, M., Hiraldo, F., Arrondo, E., Donázar, J.A., Cortés-Avizanda, A., Selva, N., Lambertucci, S.A., Bhattacharjee, A., Brewer, A., Anadón, J.D., Abernethy, E., Rhodes, O.E., Turner, K., Beasley, J.C., DeVault, T.L., Ordiz, A., Wikenros, C., Zimmermann, B., Wabakken, P., Wilmers, C.C., Smith, J.A., Kendall, C.J., Ogada, D., Buechley, E.R., Frehner, E., Allen, M.L., Wittmer, H.U., Butler, J.R.A., du Toit, J.T., Read, J., Wilson, D., Jerina, K., Krofel, M., Kostecke, R., Inger, R., Samson, A., Naves-Alegre, L., Sánchez-Zapata, J.A., 2019. Scavenging in the Anthropocene: Human impact drives vertebrate scavenger species richness at a global scale. Global Change Biology 3005–3017. https://doi.org/10.1111/gcb.14708

Spencer, E.E., Barton, P.S., Ripple, W.J., Newsome, T.M., 2020. Invasive European wasps alter scavenging dynamics around carrion. Food Webs 24, e00144. https://doi.org/10.1016/j.fooweb.2020.e00144

Sugiura, S., Tanaka, R., Taki, H., Kanzaki, N., 2013. Differential responses of scavenging arthropods and vertebrates to forest loss maintain ecosystem function in a heterogeneous landscape. Biological Conservation 159, 206–213. https://doi.org/10.1016/j.biocon.2012.11.003

Therneau, T.M., Grambsch, P.M., 2000. Modeling survival data : extending the Cox model, Statistics for biology and health. Springer, New York.

Turner, K., Abernethy, E., Conner, L., Olin, E., Beasley, J., 2017. Abiotic and biotic factors modulate carrion fate and vertebrate scavenging communities. Ecology 98, 2413–2424. https://doi.org/10.1002/ecy.1930

Turner, K.L., Conner, L.M., Beasley, J.C., 2020. Effect of mammalian mesopredator exclusion on vertebrate scavenging communities. Sci Rep 10, 2644. https://doi.org/10.1038/s41598-020-59560-9

Ward-Jones, J., Pulsford, I., Thackway, R., Bishwokarma, D., Freudenberger, D., 2019. Impacts of feral horses and deer on an endangered woodland of Kosciuszko National Park. Ecological Management & Restoration 20, 37–46. https://doi.org/10.1111/emr.12353

Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M., Getz, W.M., 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. Journal of Animal Ecology 72, 909–916. https://doi.org/10.1046/j.1365-2656.2003.00766.x

Wilmers, C.C., Getz, W.M., 2004. Simulating the effects of wolf-elk population dynamics on resource flow to scavengers. Ecological Modelling 177, 193–208. https://doi.org/10.1016/j.ecolmodel.2004.02.007

Wilmers, C.C., Post, E., 2006. Predicting the influence of wolf-provided carrion on scavenger community dynamics under climate change scenarios. Global Change Biology 12, 403–409. https://doi.org/10.1111/j.1365-2486.2005.01094.x

Wilson, E.E., Wolkovich, E.M., 2011. Scavenging: How carnivores and carrion structure communities. Trends in Ecology and Evolution 26, 129–135. https://doi.org/10.1016/j.tree.2010.12.011

Chapter 2

Necrophilous insect responses to the experimental restriction of facultative vertebrate scavengers

Chapter 2: Necrophilous insect responses to the experimental restriction of facultative vertebrate scavengers

Abstract

1. Necrophilous insects play a critical role in the decomposition of carrion and are one of the primary vectors of biomass removal in this process. However, interactions with the vertebrate scavenger guild can alter necrophilous insect colonisation and successional patterns and potentially impact carcass decay rate.
2. Understanding the interactions between the insect and vertebrate scavenger guilds is especially important in insect dominated scavenging systems where changes to insect's ability to process carrion directly affects decay rate.
3. In this study, I examined the abundance of three dominant insect taxa (ants, beetles, and flies) in response to the exclusion of vertebrate scavengers and environmental/abiotic factors (time, temperature, and elevation).
4. To do so, I placed sixteen kangaroo carcasses along a transect in a subalpine ecosystem, half inside a vertebrate exclusion cage, and then sampled the insect community for the first fifteen days of decomposition.
5. Insects were un-perturbed by the presence of vertebrate scavengers and exhibited similar patterns of colonisation and succession between treatments. Ants arrived early but were surpassed by flies and beetles towards the later sampling periods.
6. The lack of insect response to vertebrate scavenger presence highlights that environmental/abiotic factors, not competition with vertebrate scavengers, influences insect scavenging dynamics in the study system.

Introduction

Insects are major contributors to terrestrial carrion decomposition (Barton and Bump, 2019; Carter et al., 2007; DeVault et al., 2004; Ray et al., 2014). When they are at their most active, they are capable of decomposing carcasses in a matter of days (Houston, 1985; Payne, 1965). Although it is known that insects and vertebrates both compete for carrion (DeVault et al., 2004), few studies examine the effects each have on the other (Barton et al., 2013). Competition from facultative scavenging vertebrates can have a disruptive effect on insect colonisation and succession (Moleón et al., 2015; Munoz-Lozano et al., 2019) which may influence decay rate (Barton and Evans, 2017; Farwig et al., 2014). If such competition prolongs carcass persistence, it may result in unregulated nutrient flow and disease transmission (Vicente and VerCauteren, 2019). Understanding how scavenging insects are impacted by vertebrate scavengers is a key knowledge gap as their specific contributions to recycling animal biomass is not well documented (Barton et al., 2013).

Many insect species follow predictable patterns of colonisation leading to clear community succession at carcasses (Braack, 1987; Merritt and Jong, 2015). Insects provide vital contributions to decomposition via biomass removal (Barton and Evans, 2017; Payne, 1965; Pechal et al., 2014), and specialise on specific tissues in carcasses (Anderson et al., 2019). When combined, insects likely use more parts of carrion than some facultative scavenging vertebrates, although this has not been explicitly examined. The ability of insects to efficiently process carcasses is dependent on the assemblage of species feeding (Barton and Evans, 2017; Benbow et al., 2013; Farwig et al., 2014). Thus, factors that influence the assemblage of insect scavengers—such as environmental properties or competition with vertebrate scavengers—will also influence decay rate (Barton and Evans, 2017; Farwig et al., 2014; Muñoz-Lozano et al., 2019).

Insects can operate in tandem with vertebrates and microbial decomposers (Barton and Bump, 2019). Interactions among scavenger guilds may be 1) synergistic as together they provide a broader function to remove carrion, or 2) antagonistic as one guild competes with the other for the carcass (DeVault et al., 2004; Moleón et al., 2015; Ray et al., 2014; Wilson and Wolkovich, 2011). In the synergistic scenario, vertebrate scavenger's actions on the carcass may not affect insect assemblages or do so in a way that does not disrupt key insect species (Ray et al., 2014). Conversely, vertebrate scavengers could have a disruptive effect by negatively affecting insect colonisation and/or succession (Moleón et al., 2015; Munoz-Lozano et al., 2019). In this antagonistic scenario, vertebrate scavengers exclude insects by reducing the available nutrients of carrion or its window of availability. This disruption by vertebrates may restructure insect communities at carcasses and potentially carcass persistence (DeVault et al., 2003; Wilson and Wolkovich, 2011).

Insect abundance and assemblage are also mediated by abiotic factors such as ambient temperature, climate, elevation, geography, and season (Barton and Bump, 2019), which may influence carrion decay rate through the regulation of insect distribution and/or behaviour (DeVault et al., 2004; Turner et al., 2017). Insects are poikilothermic and derive thermal energy from their environment. This means their activity is positively correlated with the ambient temperature (Neven, 2000), such that season, climate, and elevation may affect insect abundance and their processing of carrion (Archer, 2004; George et al., 2013). Insects may also follow seasonal patterns in their life-cycle particularly in temperate environments producing higher periods of activity in warmer months for some species (Archer, 2003). Factors affecting insect's distribution—such as elevation and geography—can also affect carcass persistence by dictating the scavenger insect assemblage that appear on carcasses (Anderson et al., 2019). Therefore, properties of the local environment around carcasses can have profound impacts on insects found at carrion.

Scavenging by insects in temperate environments is a complex process that is limited by environmental factors and potentially influenced by vertebrate scavengers. In an Australian context, Kosciuszko National Park (NP), in south-east New South Wales, exemplifies a temperate montane ecosystem which has a diverse community of insect and vertebrate scavengers (Spencer and Newsome, 2021). In this system, key insect taxa (ants: Hymenoptera Formicidae, beetles: Coleoptera, and flies: Diptera) are likely to be critically important consumers of carrion, and will feed in tandem with vertebrate scavengers (endemic: brush-tail possums: *Trichosurus vulpecula*, corvids: *Corvidae spp.*, dingos: *Canis dingo*, eastern quolls: *Dasyurus viverrinus*, wedge-tail eagles: *Aquila audax*; exotic: cats: *Felis catus*, foxes: *Vulpes vulpes*, pigs: *Sus scrofa*) (Barton et al., 2017; Barton and Bump, 2019; Spencer and Newsome, 2021; Spencer et al., 2020). However, the extent to which vertebrates compete with insects and disrupt their patterns at carcasses in Kosciuszko NP, or temperate systems more broadly, is not well understood. This is important because disruptions to key insect scavengers can prolong carcass persistence (Farwig et al., 2014), thus interfering with the ecosystem's ability to efficiently recycle carrion.

In this study, I examined insect scavenger taxa (ants, flies, and beetles) (Anderson et al., 2019; Barton et al., 2017) and their response to the experimental exclusion of the vertebrate scavenger guild on experimentally placed carcasses in Kosciuszko NP. Vertebrate absence along with environmental factors (time, temperature, and elevation) allow for a test of whether vertebrate activity and/or presence at carrion influences insect scavenger assemblage and succession. I specifically address the following questions:

1. Does the experimental exclusion of vertebrate scavengers on carrion lead to an increase of the primary necrophilous insect taxa (ants, beetles, and flies)?
2. Does vertebrate restriction delay the timing in which insect taxa appear?
3. Does vertebrate restriction alter the composition of functional groups of necrophilous insects?
4. How do time, temperature, and elevation influence insect presence at carrion?
5. Is there any evidence that abiotic factors influence insects more than biotic factors?

Findings gathered from this study provide insight on the interactions between vertebrates and insects at carrion, and thus how scavenging food web dynamics operate in a temperate ecosystem.

Methods

Study Site

This study was conducted during January-March 2021 (summer) in Kosciuszko NP in the Australian alpine and subalpine ecotones centred around 148.489 -36.303 (Figure 21). The forest is dominated by gum trees (*Eucalyptus spp.*) with a moderate woody understory. The groundcover consisted primarily of bark from the surrounding Eucalypt spp. with occasional small forbs and grasses. The nearest Bureau of Meteorology station to the study transect is Hotel Kosciuszko which records an annual summer maximum of 18.7 with a mean of 17.8°C (±1.2) and mean annual precipitation of 1,275.4mm (Bureau of Meteorology, 2020). Summer temperatures in the lower elevations and sub-alpine regularly reach between 20-30°C (Appendix 2). Snow cover typically occurs between June through October. The study area was not burned by the most recent wildfires of 2019-2020. Kosciuszko NP is an ideal comparative analogue to temperate montane environments rigorously studied in the northern hemisphere (Independent Scientific Committee (N.S.W.), 2003).

Field Methods

I deployed 16 eastern grey kangaroo (*Macropus giganteus*) carcasses between January 2021 and April 2021. Carcasses were sourced adjacent to Kosciuszko NP from pest animal culls and from licensed harvesters following New South Wales collection guidelines. Carcasses were presented intact with exception of entry and exit wounds from firearm ordinance during collection. We deployed carcasses in eucalypt forests with similar shading along a transect. A visual and photographic comparison of canopy cover and slope was used to standardise habitat between placements. The transect was chosen within the park boundaries following the length and curves of Island Bend Fire Trail as an example of un-interrupted forest with minimal human impact. We placed sites 2 kilometres from each other.

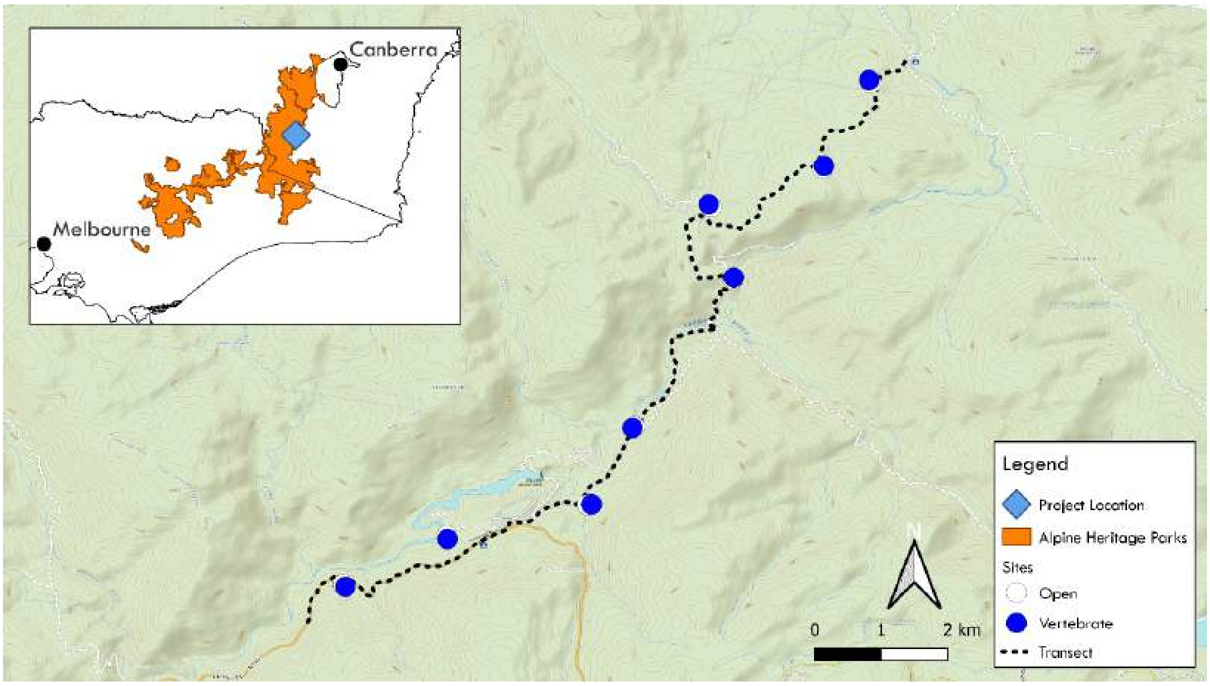


Figure 21. An overview of the project's study transect and exclusionary treatment sites in Kosciuszko National Park along Island Bend Fire Trail from the Botherum Plain to Guthega Road. The Park is in the Australian alpine region which span across southern New South Wales and eastern Victoria between Canberra and Melbourne. Kosciuszko NP occupies most of the alpine region in New South Wales.

Eight sites were placed along a continuous and forested transect; each consisting of two carcass treatments: open (exposed/no exclusion) and caged (vertebrate exclusion) (Figure 22). Open sites were placed no less than 100 metres from the road with paired caged sites 50 metres from each other carcass. To prevent vertebrate access, caged sites had a steel mesh walls (5cm aperture, 2.5mm gauge) and chicken wire (5cm aperture, 1mm gauge) with cubic dimensions (2 × 1 × 1 metres). Carcasses were monitored for the first 15 days of decomposition and visited every 72 hours to collect samples. Body condition, sex, and weight of each carcass was recorded upon deployment.

Figure 22. Scavenger exclusion treatments showing carcasses at an open site (A) with no exclusion and at a caged site with vertebrate exclusion (B).

Insect Sampling

To attain an adequate measurement of insect activity, each carcass treatment was sampled with two 120ml pitfall traps half-filled with polyethylene glycol (preservative). Traps were open for 72-hour sampling periods for the first fifteen days of decomposition (Barton and Evans, 2017; Spencer et al., 2020). Pitfall traps were placed 20cm from the carcass and level with the ground; one near the head and one near the pelvis. Contents of each paired pitfall trap were summed together to mitigate random patterns in insect behaviour.

Insects were identified and counted using an Olympus stereo microscope SZ40 model (0.67X to 5X) and web-based reference tool “What bug is that?” (CSIRO, 2012). Samples were first sorted by the following taxonomic groups: ants (Hymenoptera*: Formicidae*), beetles (Coleoptera), flies (Diptera), and other because of their known scavenging behaviours (Barton et al., 2017) and high relative abundance in collected pitfall traps (Appendix 13). Additional subgroupings of flies and beetles were identified because specific species have large impacts in decomposition (Anderson et al., 2019; Merritt and Jong, 2015). In similar studies in eucalypt forests, size differences within taxa revealed larger beetles and flies colonise carrion earlier (Barton et al., 2013; Evans et al., 2020), thus classifying beetles and flies by size may reveal separate patterns within each taxa. Subgroups consisted of 1) large flies (>10mm) and medium flies (<10mm, >5mm), 2) large beetles (>5mm) and small beetles (< 5mm), and 3) two distinct predator and scavenger beetle species (*Creophilous erythrocephalus* and *Ptomophila lacrymosa*). Large flies primarily consisted of blow flies (*Calliphora stygia*) who are early colonisers and whose maggots can consume a large quantity of carrion biomass (Anderson et al., 2019). Medium flies primarily consisted of a mix of smaller blow flies (Calliphora spp.), flesh flies (Sarcophagidae spp.), and house flies (Muscidae spp.) who may arrive later into the decomposition process and whose maggots may not consume as much carrion biomass (Anderson et al., 2019). Large beetles were a mix of Staphylinidae spp., Silphidae spp., Histeridae spp., Dermestidae spp., Trogidae spp., Scarabaeidae spp., Carabidae spp., Elateridae spp., Reduviidae spp., Pentatomidae spp.; with the top three morpho-species Silphidae spp. (53.9%), Staphylinidae spp. (18.8%), and Dermestidae spp. (16.1%) constituting 88.8% of the large beetle abundance (Appendix 28). The two most abundant beetle species, *Ptomophila lacrymosa* (Silphidae) and *Creophilus erythrocephalus* (Staphylinidae) were selected as proxies for functional diversity the beetle community. *Ptomophila lacrymosa* and its larvae are scavengers, arriving early and primarily feeding on carrion flesh but may feed upon maggots (*Diptera spp.*) (Anderson et al., 2019). *Creophilus erythrocephalus* is also an early arrival and primarily predates upon Dipteran eggs, larvae, and pupae (Anderson et al., 2019).

Data Analysis

To characterise necrophilous insect abundance and successional patterns, the predominate taxa (ants, beetles, and flies) were modelled with the experimental treatment and a mix of environmental variables first as a community, then as separate taxa, then within the subgroupings of taxa (large vs small beetles; large vs small flies; *P. lacrymosa* vs *C. erythrocephalus*). All models of insect abundance had the experimental treatment as a predictor variable as well as permutations of the abiotic variables (time, temperature, and elevation) (Appendix 14; Appendix 16; Appendix 18; Appendix 20; Appendix 23). Although the experimental design did not explicitly contain an altitudinal gradient, there was an elevation difference of approximately 500 metres and thus elevation may have an effect. Models were then selected using a corrected Akaike Information Criterion (AICc), discarding models with AICc greater than 2 from the top model and least number of explanatory variables. Independent numeric variables were scaled and mean-centred to compare values on different scales such as temperature and elevation.

Community assemblage and succession was modelled using a Permutational Multivariate Analysis of Variance (PERMANOVA, `vegan::adonis`) test of the community matrix's response to the experimental and abiotic variables. This was visualised in using Nonmetric Multidimensional Scaling (nMDS) plots comparing the open and cage treatments and then faceted by collection date to show succession. Next, to characterise individual taxonomic and subgrouping responses to the absence of vertebrates and abiotic factors, abundancies of each taxa (ants, beetles, and flies) were fit with a generalised linear mixed-effects model (GLMMs, `lme4::glmer`) with site as a random effect. Significant trends found in the GLMM were visualised using dot and box plots.

All statistical tests and analysis were conducted using `Program R` version 4 and higher (R Core Team, 2020). Multivariate analysis was performed using the `vegan` package (2.5-7) (Oksanen et al., 2022) and linear modelling was performed using the `lme4` package (1.1-27.1) (Bates et al., 2015). Multivariate model assumptions for homogeneity of groups dispersions were tested using `vegan::betadisper`. Abundance data for generalised linear modelling was assessed against a negative binomial distribution (`dnbiom`) with the `fitdistrplus` package (1.1.5) (Delignette-Muller and Dutang, 2015).

Results

Insects were monitored on sixteen kangaroo carcasses during the first 15 days of decomposition. Over the sampling period a total of 13,213 ants (17.9%), beetles (56.0%), and flies (26.8%) were collected in open (54.6%) and caged (45.4%) carcass sites. Flies were observed arriving minutes after carcass deployment. Insect abundance increased over the five sampling periods with a "peak" of 29.9% of the total insects collected during days six through nine (0-3: 4.5%, 3-6: 26.2%, 6-9: 29.9%, 9-12: 14.4%, 12-15: 25.0%; Figure 23; Appendix 13).

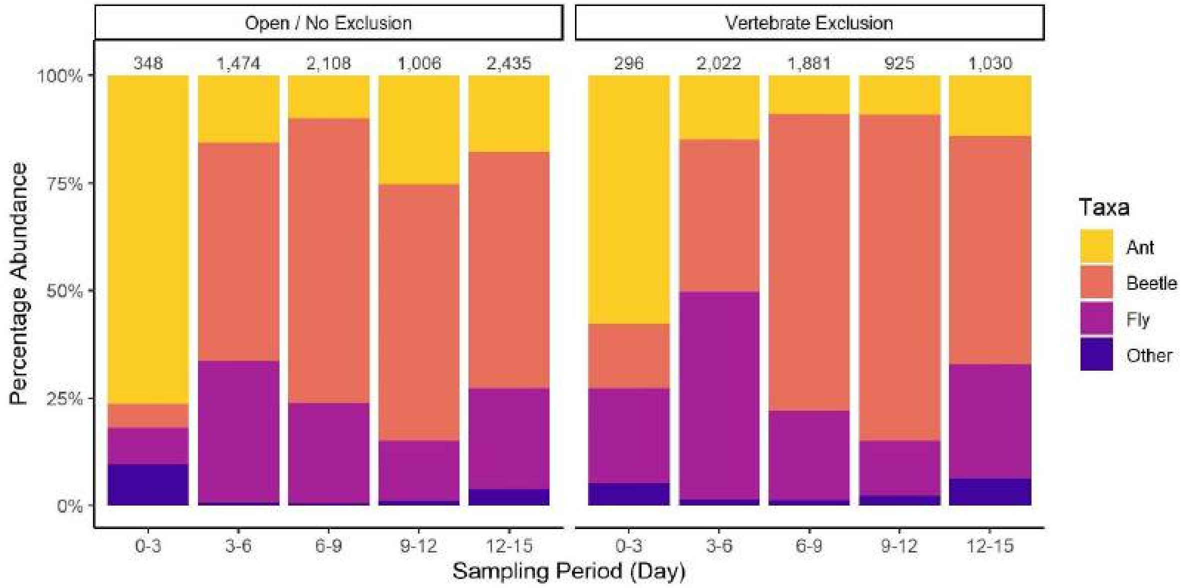


Figure 23: Percentage of abundance of insect taxa (ants, beetles, and fly) collected in pitfall traps during sampling period windows at kangaroo carcasses during the first 15 days of decay. Collection period durations were 72 hours long starting at the first day of deployment. Total insect counts are displayed above each column.

Facultative vertebrate scavengers were present and exhibited feeding behaviour during all five sampling periods at open carcass sites, the majority of which occurred during the latter half of the experiment (Appendix 30). Both the number of sites visited by vertebrates and the number of feeding events by vertebrates were low at the beginning of the five sampling periods but increased towards the end (0-3: n = 1, events = 8.6%; 3-6: n = 2, events = 1.3%; 6-9: n = 4, events = 7.8%; 9-12: n = 3, events = 6.9%; 12-15: n = 4, events = 75.4%; Appendix 27). No more than four out of the eight total carcasses were visited by vertebrates during any single sampling period.

Community Response

I found three competitive models explaining the variation within the insect community between treatments. There was no significant variation between communities in the open carcass sites and the caged sites (F_{DF1} = 1.478, R^2 = 0.013, p = 0.180; Appendix 15). However, time was the singular significant variable (F_{DF4} = 10.256, R^2 = 0.352, p = 0.001; Appendix 15) explaining community variation and models containing elevation and temperature were dropped (Appendix 14). To the larger insect community, temperature and elevation had little to do with insect assemblage. There was a large overlap among treatments but not among collection periods (Figure 24). Early colonisation of carcasses appears to be dominated by ants before shifting towards flies and beetles in later periods (Figure 25).

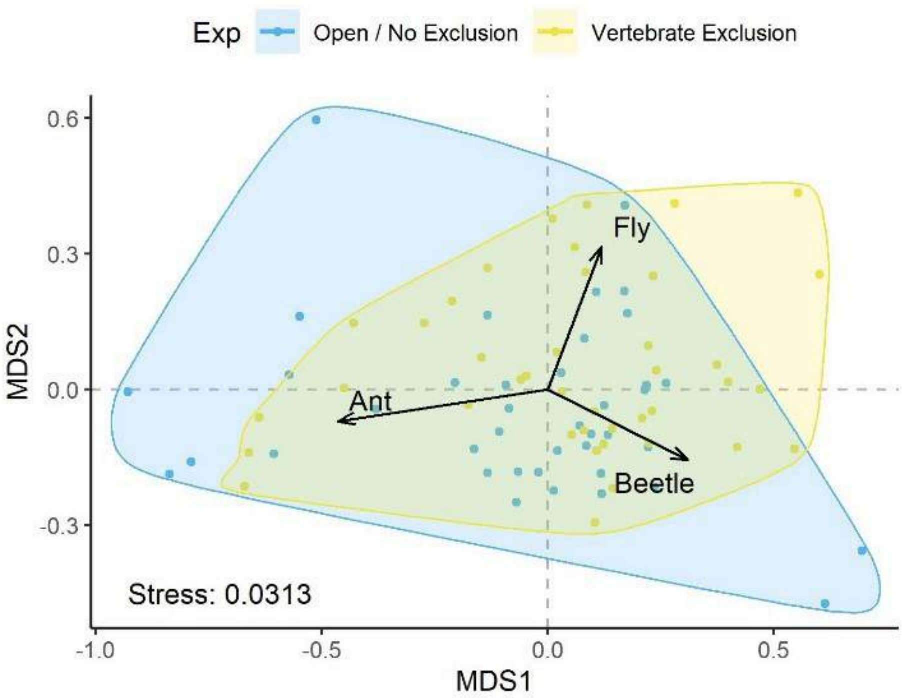


Figure 24: An MDS plot of insect community with highlighted treatment among points. Note the large overlap between treatments suggesting similarity in community composition.

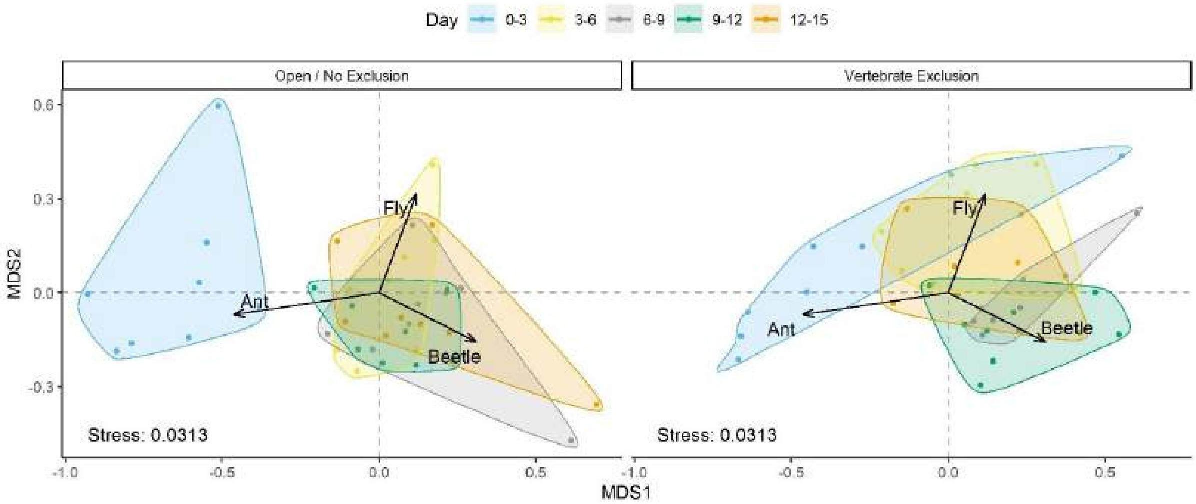


Figure 25: An MDS plot of insect community with highlighted collection period and faceted between treatment. The largest difference observed between community plots is the first day as it is heavily dominated by ants and flies. Later treatments show a shift towards beetle dominated carcasses.

Ant Response

Model permutations of the ant response to vertebrate exclusion yielded only one competitive model with no additional explainer variables (Appendix 16). The selected model (Appendix 17) showed ant abundance skewed towards open sites ($\beta = -0.530$, se = 0.234, $z = -2.262$, $p = 0.024$). However, variance of ant abundance was significantly higher at exposed sites ($\mu = 34.925$, $\sigma = 40.746$, $\sigma^2 = 1660.225$) than at caged sites ($\mu = 21.850$, $\sigma = 20.644$, $\sigma^2 = 426.182$). This was visualized in a boxplot of ant abundancies that shows several outliers with high values in the open sites that affected the model (Figure 26).

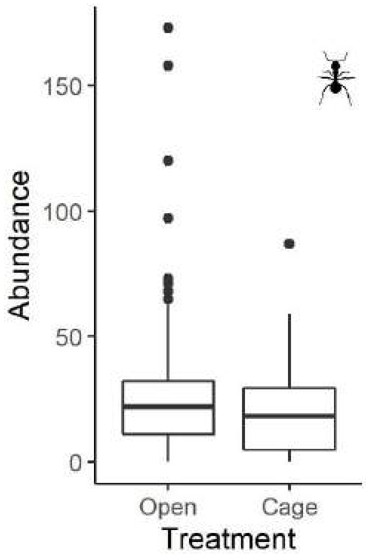


Figure 26: Ant abundance between open and caged treatments. Note the multiple outliers of high value in the open treatment. Abundance within the 25% and 75% quantiles are approximately the same between treatments.

Beetle Response

Model permutations of beetle abundance in response to treatment, time, and environmental variables yielded two competitive models (Appendix 16). Each model contained treatment, time, and temperature and an interaction between time and temperature. Elevation as an explanatory variable was present in one of the models but did not have a significant effect so the model was discarded. Beetle abundance did not have a significant response to experimental treatment ($p = 0.236$). Beetle abundance increased with time ($\beta = 0.463$, se = 0.177, $z = 2.608$, $p = 0.009$), temperature ($\beta = 0.435$, se = 0.181, $z = 2.403$, $p = 0.016$) as well as the interaction between them ($\beta = -0.950$, se = 0.096, $z = -9.930$, $p < 0.001$) (Figure 27).

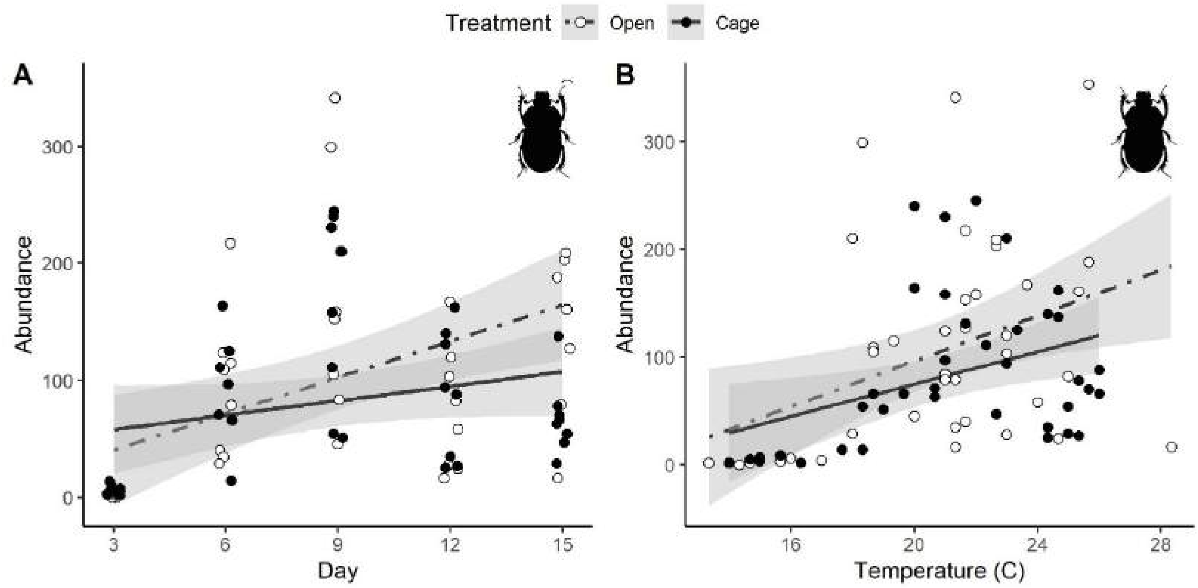


Figure 27: Beetle abundance response to time (A) and temperature (B) across open and caged carcass treatment sites. Both slopes are significant for the respective variable but are not between exclusion treatments.

For large and small beetles there were four competitive models (Appendix 18). Three were discarded due to over grouping or redundant variables. Similar to all beetles, large and small beetle abundance increased with time (β = 0.456, se = 0.151, z = 3.026, p = 0.002), temperature (β = 0.430, se = 0.155, z = 2.775, p = 0.006), and their interaction (β = -0.944, se = 0.083, z = -11.349, p < 0.001) (Appendix 19). There was no difference in beetle abundance between treatments (p = 0.149) or between large and small beetles (p = 0.739).

Much like the broader beetle taxon, the model of a select scavenger (*Ptomophila lacrymosa*) and predator (*Creophilus erythrocephalus*) beetle species appears to follow a similar pattern. With model selection this yielded three competitive models (Appendix 20). The model selected had additional interaction variables in it because of suspected differences of succession between the two beetle species. Abundance of *P. lacrymosa* and *C. erythrocephalus* did not vary between treatments (p = 0.285). *P. lacrymosa* was more abundant than *C. erythrocephalus* (β = 1.099, se = 0.181, z = 6.090, p < 0.001) and both beetles increased with time (β = 0.750, se = 0.274, z = 2.733, p = 0.006) (Appendix 21). *P. lacrymosa* showed an increase in abundance over time relative to *C. erythrocephalus* (β = -0.737, se = 0.351, z = -2.100, p = 0.036, Figure 28). There was a succession of larval *P. lacrymosa* that appear in the latter half of the collection periods and quickly grow in abundance. Abundance of these two beetle species increased with the interaction of both time and temperature (β = -1.351, se = 0.120, z = -11.242, p < 0.001).

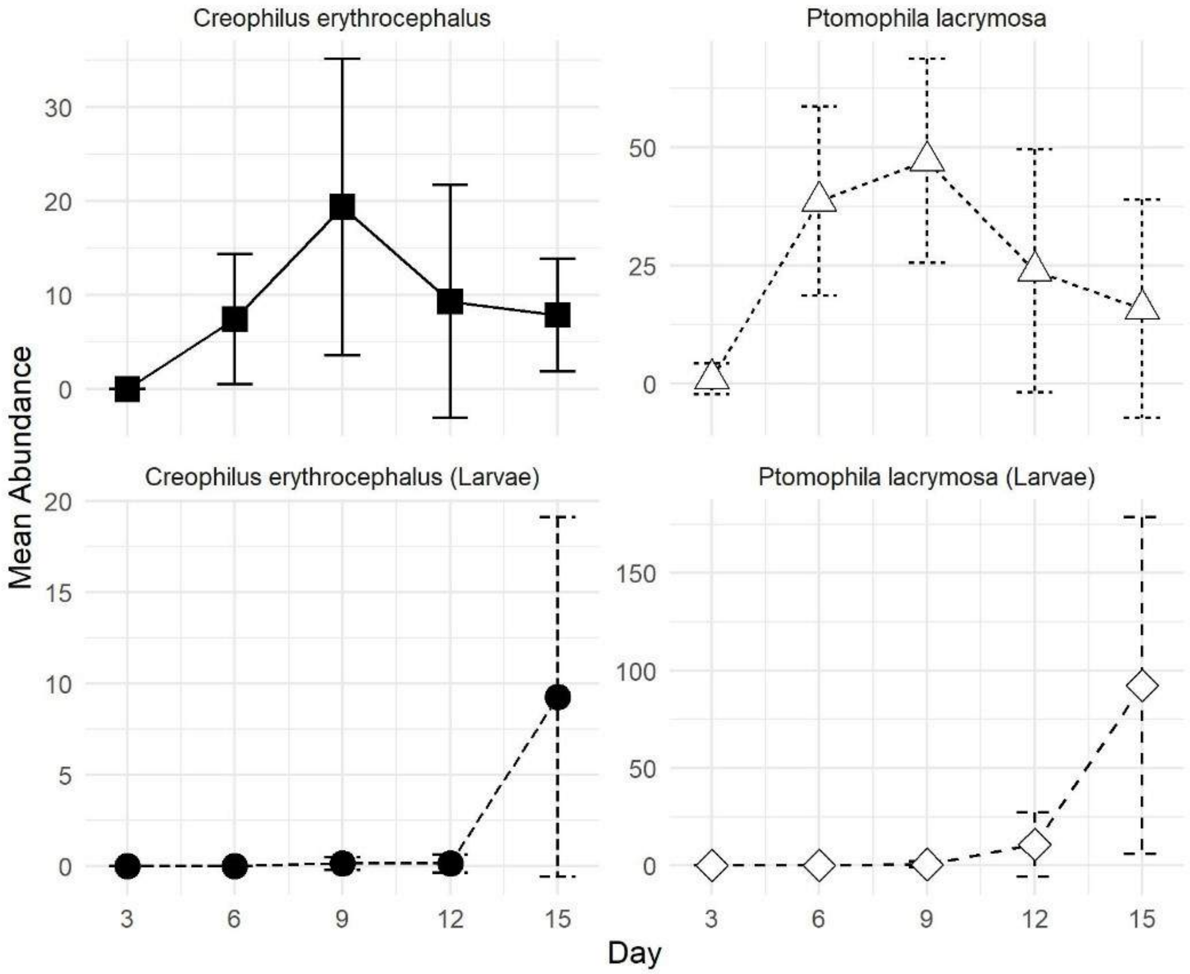


Figure 28: Two necrophilous beetle species (*Creophilus erythrocephalus* and *Ptomophila lacrymosa*) abudnance over the first fifteen days of decomposition. *C. erythrocephalus* is a specialist predator that actively feeds on insect larvae on or near carrion while *P. lacrymosa* is a scavenger that feeds directly on carrion. Note the rise in abundance of each species' larvae towards the end of the collection period.

Fly Response

Fly abundance response to the experimental treatment of vertebrates and other abiotic factors yielded two competitive models (Appendix 16). A model containing time, temperature, and their interaction showed the lowest AICc and was chosen as the most competitive (Appendix 22). Fly abundance did not differ between treatments ($p = 0.837$), nor vary with only time or temperature (Figure 29). However, fly abundance appears to have an interactive effect with time and temperature ($\beta = -0.866$, se = 0.142, $z = -6.105$, $p < 0.001$).

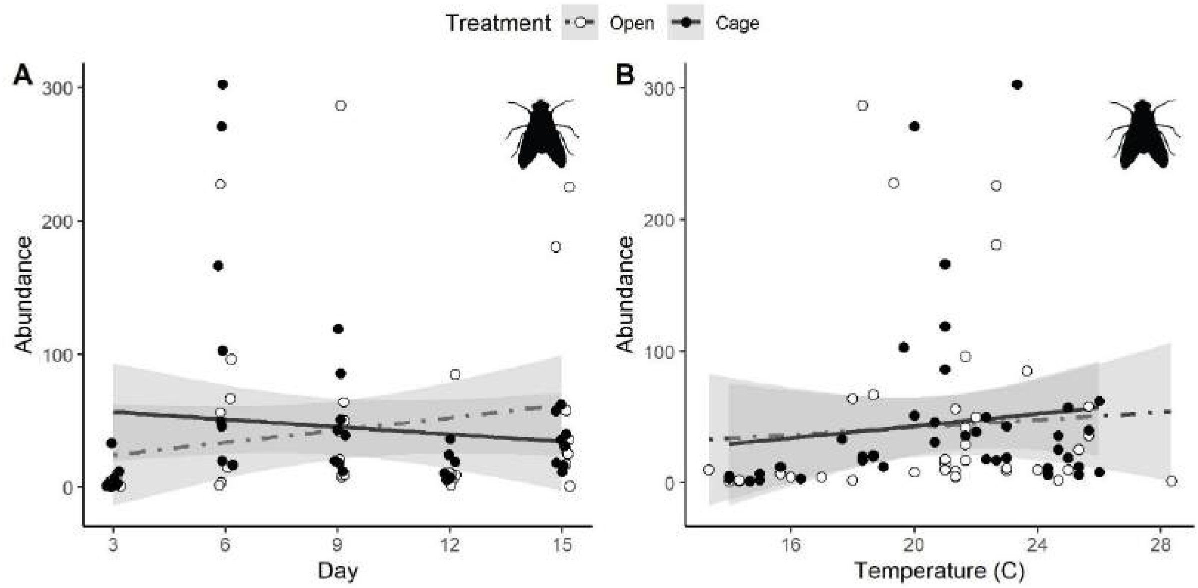


Figure 29: Fly abundance response to time (A) and temperature (B). Fly response to time and temperature were not significant on their own.

Grouping flies into large and medium sizes yielded similar abiotic effects to the larger taxon but showed a response to the exclusion of vertebrates among medium-sized flies. Comparing between taxa, treatment, and other environmental factors yielded only one competitive model (Appendix 23). In this model (Appendix 24), total fly abundance increased with time (β = 0.682, se = 0.256, z = 2.660, p = 0.008). However, this may mask the underlying trends as medium flies arrived in mass during the second collection period but decreased with time relative to large flies (β = -0.986, se = 0.326, z = -3.026, p = 0.002; Figure 30). Medium flies were more abundant in the pitfall traps than large flies (β = 1.359, se = 0.195, z = 6.976, p < 0.001). Medium flies showed a mild preference for caged sites (β = 0.392, se = 0.192, z = 2.040, p = 0.041).

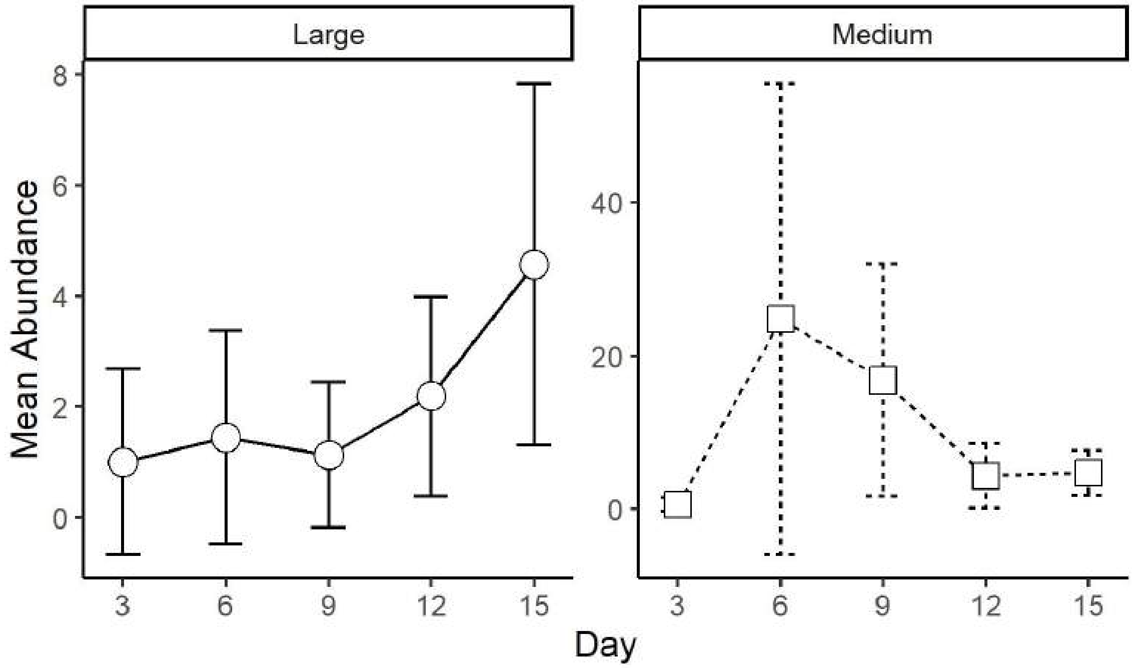


Figure 30: Abundance of large- and medium-sized flies at carcasses during the first fifteen days of decomposition. Large fly abundance increased through the duration of the trial while medium fly abundance peaked between days 6 through 9 then declined.

Discussion

Response to vertebrate absence

In this study, the abundance of necrophilous insects at broad taxonomic levels did not respond to the experimental restriction of facultative vertebrate scavengers but the select subgrouping of ants and medium-size flies may exhibit a minor preference (Appendix 14; Figure 24). The community of broadly defined insect taxa did vary as time progressed but followed similar patterns between treatments showing that succession was similar (Figure 25). This result may be due to low disturbance or visitations by facultative vertebrate scavengers during the experiment (Appendix 26). Vertebrate scavengers were slower to discover carcasses relative to insects but did exhibit an increase in abundance and feeding during the latter half of the study. Furthermore, no more than half of the carcasses were fed upon by vertebrates during a single sampling period suggesting that vertebrates, at their observed/natural distribution, in Kosciuszko NP do not influence the broader necrophilous insect community.

In this study, most insect taxa and their subgroupings were equally present at both the open and caged treatments. Exceptions to this were ants (more abundant at open sites) and medium-sized flies (more abundant at caged sites). Ant's preference for open carcasses could possibly have been due to vertebrate facilitation as fragmented carcasses enabled greater access to soft tissues. However, given the low visitations by vertebrate scavengers to open carcass sites, a more-likely possibility is the placement of some of the open carcasses may have been closer to ant nests. Indeed, ant abundance at open sites was greater but that was driven by a few outlier samples in four observations where ants were present in large quantities (Figure 26). This is consistent with ant scavengers in Australian ecosystems which are known to be an early arrival at carrion and opportunistically forage on it in close proximity to their nests rather than seek it out (Barton et al., 2017). This may explain the high abundance of ants in only a few pitfall traps as some carcasses may have been randomly placed close to ant nests.

Medium-sized flies (primarily comprised of a mix of smaller blow flies, flesh flies, and house flies), were caught in higher numbers at the caged sites. This response could be explained by either a low tolerance of vertebrate disturbance at carrion or a reduction in competition from larger flies. Medium-sized flies have a low threshold of vertebrate tolerance and displace themselves in vertebrate's presence to avoid interaction or predation. Unfortunately, the scale of sampling periods in this study was too broad to measure a timed response of insect abundance to vertebrate activities. For the second scenario, prolonged effect of carcass decay also prolonged resource availability long enough for medium-sized flies to colonise the carcass. Typically, flesh flies and house flies take longer to arrive on carcasses than blow flies (Anderson et al., 2019; Evans et al., 2020). A prolonged decay would enable a greater diversity of flies during early colonisation which may have been the case with the caged treatment. Indeed, decay within the cage treatments was observed to be slightly slower, but not significantly so (Appendix 29), and fewer maggot masses tended to form on the caged treatments based on field observations. This slight delay in carcass decomposition may have lessened competition pressures to for flesh flies and house flies allowing them to appear in greater abundance.

Response to abiotic factors

Undoubtably, the insects in this study had stronger responses to time and temperature than the absence of vertebrate scavengers. Indeed, the lack of vertebrate response suggests that insects exhibit their natural patterns of colonisation and succession without any vertebrate hindrance. Ants, beetles, flies, as well as the combined community exhibit distinct patterns to time and temperature with little preference for a particular altitude.

Necrophilous insect's response to time was quite large even across treatments and especially among beetles and flies. Colonisation and successional patterns of the insect community showed ants arriving early then progressing to a fly and beetle dominated assemblage (Figure 25). This is consistent with other studies in south-eastern Australia (Barton et al., 2017; Evans et al., 2020). Additionally, large flies and beetles were among the earliest arrivals followed by a large increase in beetle abundance (Anderson and VanLaerhoven, 1996; Bajerlein et al., 2011). Beetles and their subgroupings had the strongest successional patterns of all three taxa as they arrived quickly and became more numerous across both treatments. Interestingly, large fly abundance became more numerous in both treatments towards the end of the study as the two most abundant beetle species (*C. erythrocephalus* and *P. lacrymosa*) declined (Figure 28; Figure 30). This may be due to excess room in the pitfall traps as the adult beetles declined as flies were observed in mass throughout the study.

Insects exhibited the same positive responses to temperature across both treatments. Although temperature was not a predictor of broad community variation (Appendix 31), beetle and fly abundancies were positively correlated with higher temperatures. In congruence with previous research studies (Archer, 2004; Payne, 1965), beetles and groups of flies in this study responded positively to temperature. In the case of beetles, the response to temperature and time were almost identical, highlighting the importance of both these factors in carrion colonisation. Although flies may not have had a strong interaction with temperature in this study on a broad scale, this may be due to the sampling resolution as flies can quickly colonise or disperse. Conversely, ant abundance did not vary with temperature or elevation showing sustained activity at carcasses despite this study's range of environmental factors. This is similar to previous insect scavenger studies that showed sustained ant abundance due to ants foraging behaviours (Barton et al., 2017).

Lastly, elevation was used as a model predictor, however insects did not seem to respond to altitudinal changes. The simplest answer may be that the sites chosen did not exhibit enough of a gradient to encompass the upper limits of the sub-alpine. Although beetle and fly species can have specific altitudinal distributions (Baz et al., 2007; De Jong and Chadwick, 1999), this study captured a narrower band of elevation (Appendix 32).

Conclusion

Kosciuszko NPs insect scavenging guild is capable of consuming carrion quickly. Beetles and flies did respond positively to time and temperature while ant did not which appears to follow the paradigm of necrophilous insects in Australian ecosystems (Barton et al., 2017). Indeed, these patterns of abundance, assemblage, and colonisation were not disturbed in the slightest by vertebrate scavengers. This extreme lack of response to facultative vertebrate scavengers highlights Kosciuszko NP's heavy reliance on invertebrate scavengers to efficiently process carrion. This process of decomposition is inherently different from many ecosystems that have a dominant vertebrate scavenger guild that routinely compete with necrophagous insects (Barton et al., 2017; DeVault et al., 2004; Moleón et al., 2015). This suggests further research into the capacity of necrophagous insects to consume carrion under more extreme conditions and explore hypotheses of the effectiveness of Kosciuszko NP's vertebrate scavenging guild.

References

Anderson, G.S., Barton, P.S., Archer, M., Wallace, J.R., 2019. Invertebrate Scavenging Communities, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 45–69. https://doi.org/10.1007/978-3-030-16501-7_3

Anderson, G.S., VanLaerhoven, S.L., 1996. Initial Studies on Insect Succession on Carrion in Southwestern British Columbia. J. Forensic Sci. 41, 13964J. https://doi.org/10.1520/JFS13964J

Archer, M.S., 2004. Rainfall and temperature effects on the decomposition rate of exposed neonatal remains. Sci Justice 44, 35–41. https://doi.org/10.1016/S1355-0306(04)71683-4

Archer, M.S., 2003. Annual variation in arrival and departure times of carrion insects at carcasses: implications for succession studies in forensic entomology. Aust. J. Zool. 51, 569. https://doi.org/10.1071/ZO03053

Bajerlein, D., Matuszewski, S., Konwerski, S., 2011. Insect succession on carrion: Seasonality, habitat preference and residency of histerid beetles (Coleoptera: Histeridae) visiting pig carrion exposed in various forests (Western Poland). Polish Journal of Ecology 59, 789–797.

Barton, P.S., Bump, J.K., 2019. Carrion Decomposition, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 101–124. https://doi.org/10.1007/978-3-030-16501-7_5

Barton, P.S., Cunningham, S.A., Lindenmayer, D.B., Manning, A.D., 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia 171, 761–772. https://doi.org/10.1007/s00442-012-2460-3

Barton, P.S., Evans, M.J., 2017. Insect biodiversity meets ecosystem function: differential effects of habitat and insects on carrion decomposition. Ecological Entomology 42, 364–374. https://doi.org/10.1111/een.12395

Barton, P.S., Evans, M.J., Pechal, J.L., Benbow, M.E., 2017. Necrophilous Insect Dynamics at Small Vertebrate Carrion in a Temperate Eucalypt Woodland. Journal of Medical Entomology 54, 964–973. https://doi.org/10.1093/jme/tjw242

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Baz, A., Cifrián, B., Díaz-äranda, L.M., Martín-Vega, D., 2007. The distribution of adult blow-flies (Diptera: Calliphoridae) along an altitudinal gradient in Central Spain. Annales de la Société entomologique de France (N.S.) 43, 289–296. https://doi.org/10.1080/00379271.2007.10697524

Benbow, M., Lewis, A., Tomberlin, J., Pechal, J., 2013. Seasonal Necrophagous Insect Community Assembly During Vertebrate Carrion Decomposition. Journal of Medical Entomology 50, 440–450. https://doi.org/10.1603/ME12194

Braack, L.E.O., 1987. Community dynamics of carrion-attendant arthropods in tropical african woodland. Oecologia 72, 402–409. https://doi.org/10.1007/BF00377571

Bureau of Meteorology, 2020. Summary statistics MOUNT KOSCIUSKO (HOTEL KOSCIUSKO) [WWW Document]. URL http://www.bom.gov.au/climate/averages/tables/cw_071012.shtml (accessed 11.4.20).

Carter, D.O., Yellowlees, D., Tibbett, M., 2007. Cadaver decomposition in terrestrial ecosystems. Naturwissenschaften 94, 12–24. https://doi.org/10.1007/s00114-006-0159-1

CSIRO, 2012. What Bug Is That? The guide to Australian insect families. [WWW Document]. Taxonomy Research & Information Network. URL http://anic.ento.csiro.au/insectfamilies/ (accessed 10.18.21).

De Jong, G.D., Chadwick, J.W., 1999. Decomposition and Arthropod Succession on Exposed Rabbit Carrion During Summer at High Altitudes in Colorado, USA. J Med Entomol 36, 833–845. https://doi.org/10.1093/jmedent/36.6.833

Delignette-Muller, M.L., Dutang, C., 2015. fitdistrplus: An R Package for Fitting Distributions. Journal of Statistical Software 64, 1–34. https://doi.org/10.18637/jss.v064.i04

DeVault, T.L., Brisbin, Jr., I.L., Rhodes, Jr., O.E., 2004. Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers. Can. J. Zool. 82, 502–509. https://doi.org/10.1139/z04-022

DeVault, T.L., Jr, O.E.R., Shivik, J.A., 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102, 225–234. https://doi.org/10.1034/j.1600-0706.2003.12378.x

Evans, M., Wallman, J., Barton, P., 2020. Traits reveal ecological strategies driving carrion insect community assembly. Ecological Entomology 45, 966–977. https://doi.org/10.1111/een.12869

Farwig, N., Brandl, R., Siemann, S., Wiener, F., Müller, J., 2014. Decomposition rate of carrion is dependent on composition not abundance of the assemblages of insect scavengers. Oecologia 175, 1291–1300. https://doi.org/10.1007/s00442-014-2974-y

George, K.A., Archer, M.S., Toop, T., 2013. Abiotic environmental factors influencing blowfly colonisation patterns in the field. Forensic Science International 229, 100–107. https://doi.org/10.1016/j.forsciint.2013.03.033

Houston, D.C., 1985. Evolutionary Ecology of Afrotropical and Neotropical Vultures in Forests. Ornithological Monographs 856–864. https://doi.org/10.2307/40168321

Independent Scientific Committee (N.S.W.), 2003. An assessment of the values of Kosciuszko National Park : interim report. National Parks and Wildlife Service, Queanbeyan NSW.

Merritt, R.W., Jong, G.D.D., 2015. Arthropod Communities in Terrestrial Environments, in: Carrion Ecology, Evolution, and Their Applications. CRC Press.

Moleón, M., Sánchez-Zapata, J.A., Sebastián-González, E., Owen-Smith, N., 2015. Carcass size shapes the structure and functioning of an African scavenging assemblage. Oikos 124, 1391–1403. https://doi.org/10.1111/oik.02222

Munoz-Lozano, C., Martin-Vega, D., Martinez-Carrasco, C., Sanchez-Zapata, J.A., Morales-Reyes, Z., Gonzalvez, M., Moleon, M., 2019. Avoidance of carnivore carcasses by vertebrate scavengers enables colonization by a diverse community of carrion insects. PLoS One 14, e0221890. https://doi.org/10.1371/journal.pone.0221890

Muñoz-Lozano, C., Martín-Vega, D., Martínez-Carrasco, C., Sánchez-Zapata, J.A., Morales-Reyes, Z., Gonzálvez, M., Moleón, M., 2019. Avoidance of carnivore carcasses by vertebrate scavengers enables colonization by a diverse community of carrion insects. PLOS ONE 14, e0221890. https://doi.org/10.1371/journal.pone.0221890

Neven, L.G., 2000. Physiological responses of insects to heat. Postharvest Biology and Technology 21, 103–111. https://doi.org/10.1016/S0925-5214(00)00169-1

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M.D., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlinn, D., Ouellette, M.-H., Cunha, E.R., Smith, T., Stier, A., Braak, C.J.F.T., Weedon, J., 2022. vegan: Community Ecology Package.

Payne, J.A., 1965. A Summer Carrion Study of the Baby Pig Sus Scrofa Linnaeus. Ecology 46, 592–602. https://doi.org/10.2307/1934999

Pechal, J.L., Benbow, M.E., Crippen, T.L., Tarone, A.M., Tomberlin, J.K., 2014. Delayed insect access alters carrion decomposition and necrophagous insect community assembly. ECOSPHERE 5. https://doi.org/10.1890/ES14-00022.1

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ray, R.-R., H. Seibold, M. Heurich, 2014. Invertebrates outcompete vertebrate facultative scavengers in simulated lynx kills in the Bavarian Forest National Park, Germany. Animal biodiversity and conservation 37.

Spencer, E., Newsome, T., 2021. Dingoes dining with death. Australian Zoologist 41, 433–451. https://doi.org/10.7882/AZ.2021.008

Spencer, E.E., Barton, P.S., Ripple, W.J., Newsome, T.M., 2020. Invasive European wasps alter scavenging dynamics around carrion. Food Webs 24, e00144. https://doi.org/10.1016/j.fooweb.2020.e00144

Turner, K., Abernethy, E., Conner, L., Olin, E., Beasley, J., 2017. Abiotic and biotic factors modulate carrion fate and vertebrate scavenging communities. Ecology 98, 2413–2424. https://doi.org/10.1002/ecy.1930

Vicente, J., VerCauteren, K., 2019. The Role of Scavenging in Disease Dynamics, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 161–182. https://doi.org/10.1007/978-3-030-16501-7_7

Wilson, E.E., Wolkovich, E.M., 2011. Scavenging: How carnivores and carrion structure communities. Trends in Ecology and Evolution 26, 129–135. https://doi.org/10.1016/j.tree.2010.12.011

Conclusion

Findings and Implications of Scavenging in Kosciuszko National Park

Conclusion: Findings and Implications of Scavenging in Kosciuszko National Park

Death is an artifact of life.

Overview

Carrion (the by-product of life) presents an opportunity for a plethora of specialised organisms to utilise the remains (Carter et al., 2007; Olea et al., 2019b). This phenomenon—scavenging—is important as it supports the communities of organisms that consume it, recycles nutrients back into the ecosystem, and reduces transmission of diseases and parasitoids that may be present at carrion (Barton et al., 2013; Ogada et al., 2012; Vicente and VerCauteren, 2019; Wilson and Wolkovich, 2011). When terrestrial scavenging is optimised, microbial, insect, and vertebrate scavengers operate in tandem (often with intricate interwoven interactions) to decompose carrion (Barton and Bump, 2019; Benbow et al., 2015a). However, disruptions to these scavenger assemblages may result in prolonged carcass decay (Huijbers et al., 2015; Payne, 1965; Pechal et al., 2014).

Through this research I have characterised the contributions insect and vertebrate scavengers provide to accelerate carcass decay in Kosciuszko NP. This research shows the Australian Alps' heavy reliance on necrophilous insect communities to efficiently process carrion that is not well supplemented from a small vertebrate scavenger assemblage (Chapter 1). This suggest there is limited functional redundancy between insect and vertebrate scavenger guilds to efficiently remove carrion biomass during cold seasons. Because Kosciuszko NP's ability to process carrion is linked to necrophagous insect behaviour, environmental changes that impact insect behaviours also impact decay rates. This finding is both important as 1) an ecosystem indicator that contextualises the Australian Alps' necrobiome in comparison to other ecosystems, and 2) a tool for natural resource managers to use in determining how to care for the unique fauna in Kosciuszko NP.

Scavenging Guild Dynamics of Kosciuszko National Park

Summary of Findings

In total, this study experimentally placed eighty-eight kangaroo carcasses (2,425kg in total; Table 6) with different exclusionary treatments in Kosciuszko NP in four seasonal replicate deployments from March 2020 through April 2021. I measured how decay rates of carcasses responded to the experimental treatment of open (no exclusion), vertebrate exclusion, and vertebrate + insect exclusion to assess how each scavenger guild (microorganisms, insects, and vertebrates) contributed to carcass decomposition. From this I found carcasses in cold seasons decayed at a much slower rate than warm seasons and that the vertebrate scavengers that fed on the carcasses during all seasons did little to accelerate decay.

For Kosciuszko NP this means, decay rates are strongly dependent on the time of the year the carcasses appear and are accelerated by scavenging insects (Figure 17). Necrophilous insects consume carrion quickly but have a limited window in which they are active that largely depends on warm temperatures (Figure 18; Figure 19). Although facultative vertebrate scavengers fed on all carcasses, their effect on decay rate was negligible. Indeed, vertebrate's presence at carcasses did not alter scavenging insect's natural patterns (Figure 24; Figure 25) and suggests between the two guilds there is either a very weak or non-existent competitive relationship. Ultimately, these results reflect an insect dominated scavenging regime that may be supplemented by vertebrate scavengers but whose contributions to decomposition are ecologically negligible (Figure 20). These findings have important implications that show decomposition is optimised in late spring through summer (Figure 17).

A Global Comparison of Australia's Necrobiome

Although scavenging is a process found globally, the assemblage of Australia's scavenger species is ecologically distinct from some other ecosystems due to its low vertebrate diversity and heavy reliance on necrophilous insects (Barton et al., 2017; Braithwaite, 1990; Read and Wilson, 2004). Therefore, it is important to understand Australia's necrobiome in context. The Australian necrobiome is dominated by a diverse group of insect scavengers with a low diversity of vertebrate scavengers (Braithwaite, 1990; Read and Wilson, 2004; Sebastián-González et al., 2019). In addition, some vertebrate scavengers have been persecuted, further reducing their abundance and thus functionality in carrion recycling (Sebastián-González et al., 2019). This is in contrast to many ecosystems that have greater vertebrate scavenger diversity or abundance or contain obligate scavengers and consequently more competition for carrion resources (DeVault et al., 2004; Moleón et al., 2015; Wilson and Wolkovich, 2011).

Due to the low diversity of vertebrate scavengers, Kosciuszko NP's necrobiome is most similar to temperate ecosystems with few apex vertebrate predators that also scavenge. In a study of scavenging communities in Bavarian Forest National Park, Germany (a temperate montane forest), scavenging was primarily driven by insects during summer months (Ray et al., 2014). Similar to Kosciuszko NP's scavenger guilds, insects consumed carrion biomass quickly and vertebrate's contribution to carrion removal was "of minor impact". The study by Ray et al (2014) in Bavarian Forest National Park, Germany described the primary vertebrate scavengers as corvids (*Corvus corax*), Eurasian lynx (*Lynx lynx*), red fox (*Vulpes vulpes*), and wild boar (*Sus scrofa*) with lynx consuming the most biomass out of the four. This resembles Kosciuszko NP's vertebrate scavenger assemblage as most of the scavenging done by vertebrates came from mesopredators. The lack of a large apex vertebrate predator regularly visiting carcass sites monitored may have led to a de-structured vertebrate assemblage shifting carcass consumption towards mesopredators and the insect guild

(Wilson and Wolkovich, 2011). Thus, in both studies, insects consumed carrion efficiently without competition by large vertebrates in warm seasons and carcasses persisted for longer periods during colder seasons.

Kosciuszko NP’s low vertebrate diversity and lack of apex scavengers is in stark contrast to ecosystems with many apex vertebrate species that can compete with invertebrates for carrion biomass (Figure 31). In a study of South African scavenger assemblages, Moleón et al (2015) found that spotted hyena (*Crocuta crocuta*) and vultures (Accipitridae) consumed most carrion biomass with negligible effects from invertebrate scavengers (Moleón et al., 2015). There, vertebrate abundance and diversity at carrion was greater than that found in this study of Kosciuszko NP’s scavenger assemblages. The South African scavenger assemblage had more structure that was enforced by apex vertebrate predators and may have led to a more stable and functional vertebrate scavenger guild compared to Kosciuszko NP’s (Wilson and Wolkovich, 2011). This comparison is useful because monitoring scavengers can be used as an indicator for ecosystem functionality (Newsome et al., 2021). This suggests that although current scavenging by vertebrates in Koscisuzko NP may not be ecologically impactful, this may not be the “normal” and that disruption to the vertebrate assemblage may be resulting in reduced competition with insect scavengers for carrion resources.

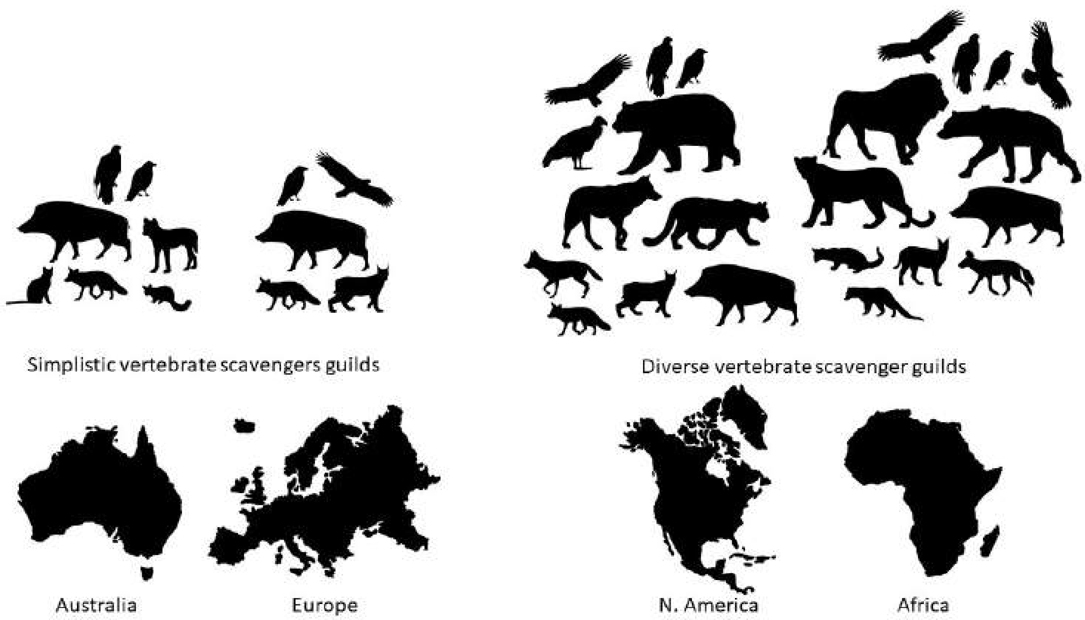


Figure 31: A conceptual overview of vertebrate scavenging guild diversity among varying ecosystems. Diverse scavenger assemblages with apex predators create community structures and support biodiversity (Wilson and Wolkovich, 2011). Consequently, carrion recycling may be more resilient in these ecosystems. Vertebrate scavenger species displayed are represented from a limited set of scavenger studies and may not reflect the complete diversity of each ecosystem. Australia: (Spencer and Newsome, 2021); Europe: (Ray et al., 2014); N. America: (Beasley et al., 2019); Africa: (Moleón et al., 2015)

A Historical Context of Australia's Necrobiome

Australia lacks a diverse vertebrate scavenger assemblage (O'Brien et al., 2007; Read and Wilson, 2004) that may be ill-adapted to process the immense quantity of carcasses that are generated annually. In our modern era, not only do carcasses come from natural sources, such as disease and predation, but also from artificial sources such as lethal control or road-strikes. Australia's endemic scavenger assemblage are comprised of animals that evolved in nutrient-poor ecosystems and may not have been adapted to an overabundance of carrion which is occurring now (Bird et al., 2013; Orians and Milewski, 2007). In a detailed history of Australia's ecology and evolutionary history, Orians and Milewski (2007) theorise the origin of Australia's unique flora and fauna stem from the continents nutrient poor soils and prolonged geologic isolation (Orians and Milewski, 2007). This led to the adaptation of hearty, defensive plant species that dissuaded herbivory allowing for fuel build-up and intense fires. The large herbivores consuming this tough plant matter may have also been on the decline due to an increasing arid environment (Bird et al., 2013) suggesting there may have been low densities of megafauna (and thus carrion). The Australian necrobiome may therefore have been adapted to recycle carrion at low spatial densities.

Australian flora and fauna assemblages have undergone a rapid change with human colonisation events and the spread of exotic invaders (Bird et al., 2013; Cook, 2021; Lawrence and Davies, 2011). Pre-western colonisation brought with it a change in fire regime and an accompanying apex predator (the dingo). This shift brought vertebrate extinctions to mainland Australia (Bird et al., 2013) including an apex scavenger, the Tasmanian devil (Brown, 2006). During this period, dingoes established themselves as the top-predator on mainland Australia, replacing the thylacine (*Thylacinus cynocephalus*) (Dickman, 1996). As a result, they likely re-structured ecological communities (Dickman, 1996; Fillios et al., 2010; Spencer and Newsome, 2021).

Western colonisation brought about additional changes to Australian ecosystems that in turn may have altered the necrobiome. These key changes including 1) an alteration of the fire frequency, 2) industrial agriculture and livestock, 3) introduction of exotic invaders, and 4) industrialised animal controls may have altered the quantity of carrion and influenced particular scavenger species (Cook, 2021, 2019; Gill, 1975; Lawrence and Davies, 2011; van Eeden et al., 2019). Since western colonisation, many extinctions of vertebrates (Woinarski et al., 2019) as well as reductions in habitat (Bradshaw, 2012) have restructured some ecosystems to favour livestock and other herbivores. This restructuring can be seen with great abundance of macropods that favour grazing lands and a reduction of dingoes where they present a threat to livestock (van Eeden et al., 2019). Additionally, the introduction of exotic game, which rapidly colonised beyond control, further skewed many Australian ecosystems to consist of many prey species without an effective apex predator (Dickman, 1996; Forsyth et al., 2019;

Lawrence and Davies, 2011; Newsome, 1990). Thus, the current context of the Australian necrobiome is such: some endemic vertebrate scavengers (that are adapted for nutrient-poor strategies) are reduced in number and this has occurred alongside an increase in large carrion biomass from both exotic invaders (such as deer and feral horses) and elevated populations of native herbivores (macropods). This overabundance of large herbivore carcasses and a lack of a functional vertebrate scavenger guild potentially skews Australian scavenging communities towards being dominated by insects.

Reasons For a Lack of Vertebrate Response

This study clearly shows that the absence of vertebrate scavengers at carrion 1) did not significantly reduce carcass persistence and 2) did not illicit responses from the necrophilous insect community. However, in many other ecosystems there is well documented competition between vertebrate and insect scavengers (Hill et al., 2018; Houston, 1985; Munoz-Lozano et al., 2019; Sebastián-González et al., 2016). Where there is a great diversity of vertebrate scavengers, insects typically consume less biomass as competition for resources is greater (Munoz-Lozano et al., 2019; Sebastián-González et al., 2016). However, this study shows vertebrates in Kosciuszko NP do not appear to compete with insects for carrion biomass and have minor impact on carcass decay. Thus, the lack of response that was seen between each carcass treatment monitored may be explained by different scenarios of how vertebrate scavengers function in this ecosystem (Table 5).

1. The inherent guild of vertebrate scavengers do not dominate use of carcass resources.
2. An oversupply of carrion may have resulted in low rates of vertebrate scavenging on individual carcasses monitored.
3. The vertebrate scavenger assemblage is dominated by smaller mesoscavangers, with very few apex scavenging visiting carcass sites.
4. Apex facultative vertebrate scavengers are unable to find carrion efficiently.

In the first scenario, facultative vertebrate scavengers in Kosciuszko NP may not have or never dominated the use of carcass resources. Although many vertebrates within Kosciuszko NP are known to scavenge and are distributed throughout the park, they may not consume carrion in enough quantity to disturb or compete with the local insect community. This is much like the scavenging dynamics described by Ray et al (2014) [see section “A Global Comparison of Australia’s Necrobiome”]. In Kosciuszko NP, the vertebrate scavenger guild primarily consists of mesoscavengers who may not structure the scavenging food web dynamics to the same extent as apex scavengers (Wilson and Wolkovich, 2011). The result is suboptimal consumption of carrion by the vertebrate scavenger guild when insects are not as common during cooler periods. Additionally, scavenger species within

Kosciuszko NP are not well documented and it is suggested that further research into their behaviour, species richness, and populations would be ideal for understanding which species have the greatest effect on carcass persistence.

In the second scenario, Kosciuszko NP may be saturated with carrion from natural and/or anthropomorphic sources that may overwhelm vertebrate scavengers. This would shift scavenging assemblages at carrion towards insect decomposers as they are able to visit all carrion quickly and consume it completely. This would explain the low vertebrate visitation rates at carrion as facultative vertebrate scavengers are not as efficient at locating carrion as insects. However, the abundance of carrion within Kosciuszko NP has not yet been quantified and this suggests an avenue of research to determine carrion abundance and sources. Understanding how much and where carrion comes from is important especially in cases of anthropogenic influence. A study of kangaroo carrion from agricultural culling in Western Australia suggested that the overabundance of carcasses could support an artificially high populations of corvids and invasive red foxes (Read and Wilson, 2004). If carrion from artificial sources remains high then this may elevate vertebrate scavengers beyond a natural capacity or change their behaviour (Newsome et al., 2015), although the low vertebrate scavenging rates documented in Kosciuszko NP suggests this is not occurring yet.

Another explanation of low vertebrate scavenging rates in carrion saturated ecosystems may be that this vertebrate assemblage is unable to consume enough biomass from each carcass to accelerate decay. All open sites were fed upon by vertebrate scavengers throughout the decay. However, the large mass of the carcasses may have proved too much for the vertebrates to efficiently consume. Smaller carcasses tend to be utilised more completely by vertebrate scavengers than large carcasses (Moleón et al., 2015) suggesting that vertebrates in this study may have reached their limit of consumption. This suggests a carcass size threshold at which vertebrate scavengers are unable to remove biomass (Figure 32). As vertebrate scavengers in Kosciuszko NP reach their limit of how much biomass they can consume from carrion, this shifts scavenger assemblages towards insect guilds as they are more prevalent in the environment.

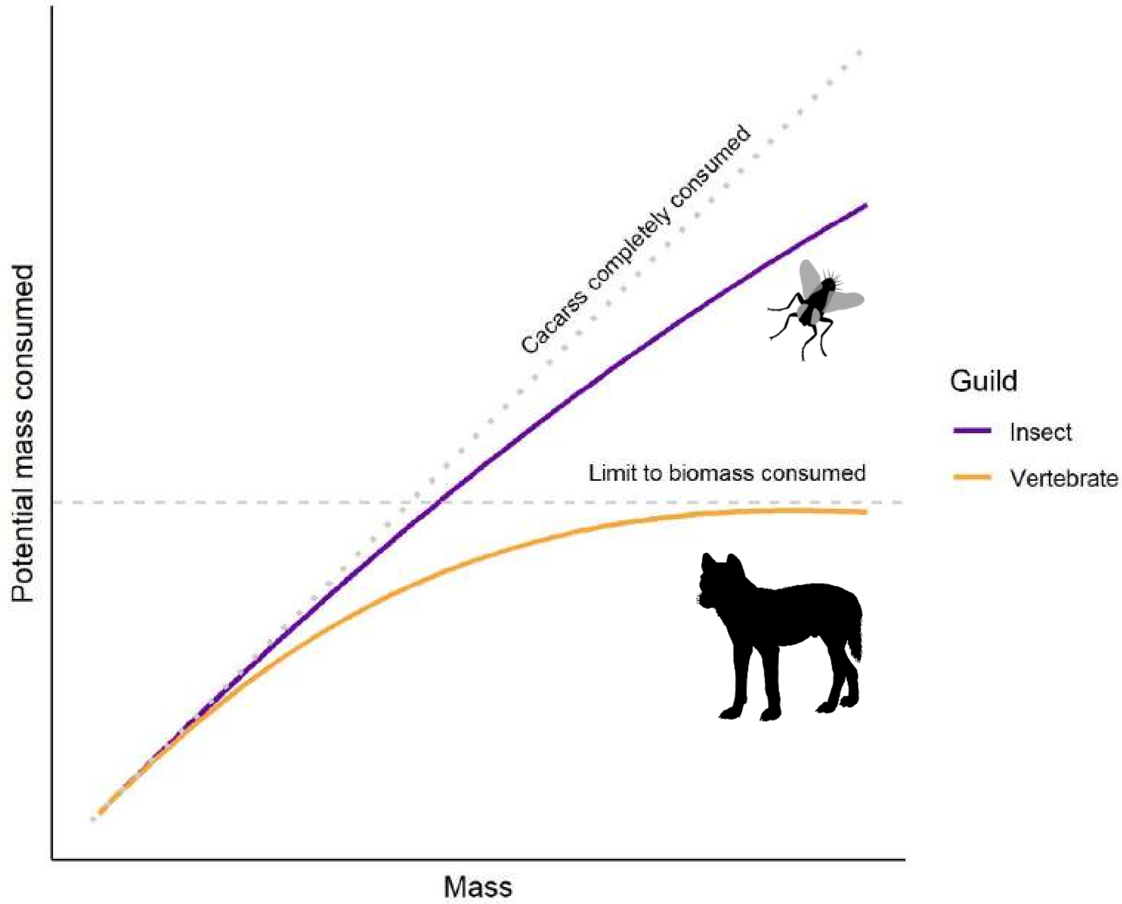


Figure 32: Vertebrate scavenger consumption limit hypothesis. As carrion mass increases vertebrate's ability to consume carrion decreases revealing a limit to the amount of biomass vertebrate scavengers can consume on a single carcass.

In the third scenario, Kosciuszko NP's vertebrate scavenger guild is dominated by mesoscavengers. Vertebrate scavengers may have had a historical role in carrion consumption but changes to the vertebrate assemblage may have resulted in this guild's inability to remove carrion efficiently. Terrestrial necrobiomes are often structured by apex vertebrate scavengers whose trophic interactions influence scavenger species assemblage (Cunningham et al., 2018; Wilson and Wolkovich, 2011). For example, declines in an apex scavenger, the Tasmanian devil, resulted in carrion availability to meso-scavengers (Cunningham et al., 2018). The predominate apex-scavengers in Kosciuszko NP is the dingo, which is actively controlled by wildlife managers. This could have a cascading trophic consequence, one of which may be a reduction in competition at carrion. If this is the case, this may have shifted carrion removal from the vertebrate to mesoscavengers.

The fourth and final scenario may be that Kosciuszko NP's vertebrate scavengers have low rates of carcass discovery allowing for insects to consume carrion before vertebrates arrive. Carrion is ephemeral and has a short window of availability which favours specialist scavengers who can meet the energy requirements of discovering carrion (Moleón et al., 2019). Because necrophilous insects are often distributed more ubiquitously than vertebrates and are specialised in consuming carrion, they are almost always the first animals to colonise a carcass (Anderson et al., 2019; Payne, 1965). Their early arrival allows for them to process the carcass before vertebrate scavengers can arrive (Ray et al., 2014). In Kosciuszko NP, this favours invertebrate scavengers and potentially corvids as their distribution and ability to locate carrion are less of a barrier than other mammalian vertebrate scavengers. This skews carcass use towards the insect scavenger guild as they comprise the majority of the early discoveries of carcasses.

Table 5: Hypotheses for the lack of vertebrate scavenging contributions to biomass loss during cold seasons.

Hypothesis	Description
1: Vertebrate non-compliance	Vertebrate scavengers are established within Kosciuszko NP, however, they do not interact with carrion especially in winter (Peers et al., 2020).
2: Mesoscavenger dominant system	Vertebrate scavengers are present, but the guild is dominated by mesoscavengers. Apex predators can have an oversized impact on biomass removal when they scavenge (Wilson and Wolkovich, 2011) but their presence in Kosciuszko NP is limited. This disturbance within vertebrate scavengers could produce inefficiencies in scavenging yielding longer carcass persistence (Huijbers et al., 2015).
3: Carrion oversaturation	Vertebrate scavengers may have an impact on carrion removal but may be ‘choosey’ when consuming carrion because it is a common resource. Efforts to reduce pest herbivores species could be saturating the carrion supply beyond what vertebrate scavengers can process.
4: Acquisition failure	Vertebrate scavengers are not adept at locating carcasses efficiently. Carrion is an ephemeral resource that appears stochastically and therefore hard to utilise. The facultative vertebrate scavengers of Kosciuszko NP may be able to acquire carcasses that appear naturally but were unable to locate carcasses experimentally placed for this study. Additionally, factors effecting vertebrate discovery rates such as decreased smell due to suppressed insect and microbial activity or dispersion properties could be modulated by colder temperatures (DeVault and Rhodes, 2002; Smith et al., 2017).

Limitations of Research

Like all science projects, this project has limitations. The practicalities of bringing this project to fruition has not been without constraints. Stochastic events and practical solutions contributed to this project’s limitations and should be considered when concluding meaning from these results. Thus, this study encapsulates a small but important portion of decomposition and furthers our understanding of a small but important aspect of scavenging communities of the Australian sub-alpine. The following is a discussion of this project's constraints and future considerations when conducing similar scavenging research.

The first and foremost complication to this study was the tenacity of necrophilous insect scavengers and their ability to infiltrate the protective layering around the insect exclusion treatment. Thus, the insect exclusionary treatment had a suppression effect on insects but not a total exclusionary one. Observations of the carcasses within meshed cages during the first fifteen days of the summer replicate showed fly larvae and beetles breached the aluminium mesh and gaining access to the carcass. Carcasses remained in the early/bloat stage slightly longer (Figure 33) but ultimately decayed at the same rates as treatments without the insect meshing. The tenacity of the insects highlighted Kosciuszko NP's reliance on insect scavengers to process carrion but hindered this project's ability to fully quantify their contribution to decomposition relative to microbial scavengers. Microbes process deceased animal tissue but are unable to remove biomass in quantities that insect or vertebrate scavengers do (Barton and Evans, 2017; Payne, 1965; Pechal et al., 2014). Thus, any biomass removal in caged trials may be attributed in part to insect scavengers.

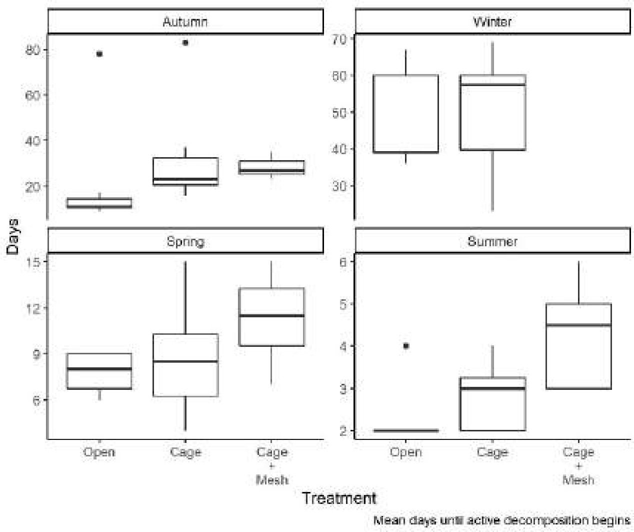


Figure 33: Mean days at which active decomposition begins. Note that in spring and summer replicates the vertebrate + insect exclusion treatment (Cage + Mesh) remained in the early/bloat stage longer and took longer to reach active decomposition.

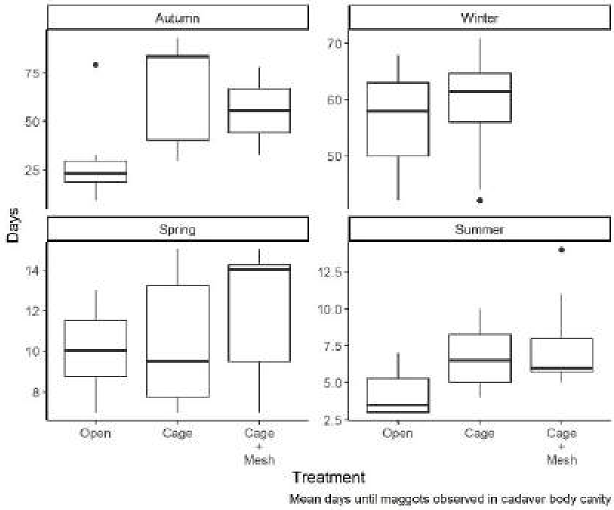


Figure 34: Mean days at which maggots were observed active in the body cavity of the cadaver. Despite carcasses reaching the early/active stage slightly sooner as indicated in Figure 33, maggots appearing in the chest cavity of the cadavers occurred at similar times.

This study, although arduous and rewarding, has a low sample size because of the extreme effort taken to set up and deploy equipment in a reliable and replicable way. Eight paired carcass sites (twenty-four carcasses per replicate) were chosen because that was the upper limit of what could physically be deployed in a single between two graduate students and a few willing volunteers. This meant physically lifting many hundreds of kilograms of kangaroos (Table 6) through difficult terrain and thick wooded understory. The deployment of carcasses for each replicate took a three-to-five-person team between twelve to fourteen hours to set up. Although more samples may have improved the robustness of some of the statistical analyses, decay rates of carrion were adequate for the performed tests. Adding further samples possibly could have boosted test accuracy but may not have yielded any further knowledge.

Table 6: Kangaroo biomass totals used in each replicate

Season	Biomass (kg)
Autumn	736
Winter	467
Spring	583
Summer	639
Total	**2,425**

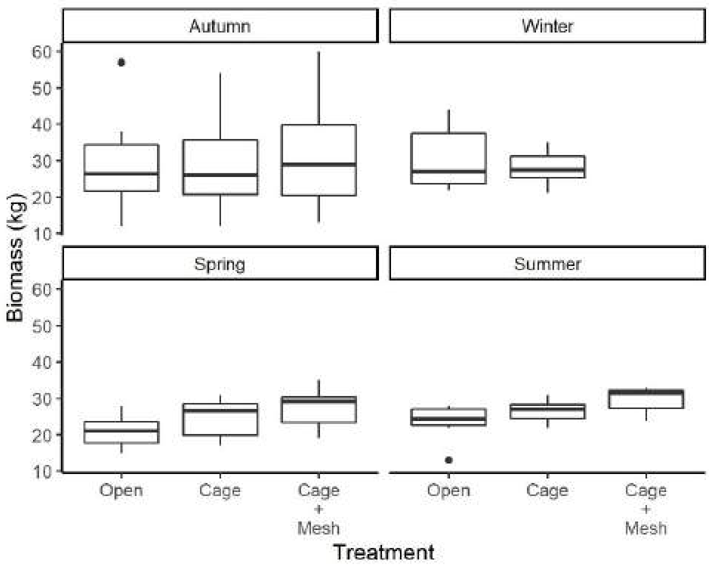


Figure 35: Mean kangaroo carcass weights used in each replicate.

This study looks at a narrow but important portion of the necrobiome by examining only large mammalian carcass decomposition. Although carrion ranges in size, this study focused on larger carcasses because of a “feral invasion” of large ungulates into the Australian Alps. Not only do deer and horses degrade native flora in the Australian Alps (Ward-Jones et al., 2019), but they leave behind many carcasses that the endemic vertebrate scavenger guilds have difficulty processing. This surplus of carrion may gradually lead to a shift in the vertebrate scavenger guild as endemic species lose their naivety to the invaders but may favour other invasive scavengers such as red fox (Forsyth et al., 2019; Newsome et al., 2015; Read and Wilson, 2004). This study is a step towards characterising Kosciuszko NP’s necrobiome and addressing the need to understand its vertebrate scavengers in detail to predict the changes in assemblages that may be underway.

A clear result from this study is the annual trends in decay rates; carcasses appearing in colder seasons will last until conditions warm (Figure 17). For the autumn and winter replicates decay rates were assessed but their decomposition to disintegration was longer than the experimental window in which to assess it. Although decay rates were significantly reduced in colder months, there was an observable acceleration of decay in the winter replicate as temperatures rose allowing for maggot activity towards the end of the experiment seen on the time lapse imagery. If carcasses were observed until their complete disintegration in the autumn and winter replicates, then this may have provided unequivocal evidence for Kosciuszko NP’s reliance on insect scavengers as well as a temperature range at which accelerated decomposition occurs. Knowing when decay will accelerate could provide a clear calendar date for natural resource managers to utilise to schedule feral controls during optimal decomposition conditions. This suggests further study into carrion decomposition during cold conditions that reflect when many feral control programs are conducted.

Koscluszko NP is an actively managed park that routinely controls for feral ungulates and canids (New South Wales et al., 2006). This is a direct manipulation of the necrobiome creating both a surplus of carrion and a reduction of available vertebrate scavengers. It is not clear whether this may have impacted the vertebrate scavenger guild in this project as these controls happen annually. Although unlikely, it's possible these animal controls may have impacted vertebrate scavenger's ability to locate and consume the experimental carrion. This suggests further research into areas with and without animal controls with the intent of contrasting vertebrate scavenger assemblages and their impact on carrion decay rates. If decomposition is different between the two assemblages, this may suggest an anthropogenic impact is negatively affecting vertebrate scavenger's functionality.

Future Predictions and Research Directions

Predictions

As the Anthropocene marches onward and human impact on ecosystems near Kosciuszko NP are continually affected, the park faces many dramatic changes to its scavenger guilds and their functionality (Sebastián-González et al., 2019). Major issues known to researchers and park managers include an invasion by feral animals, destabilisation of mammalian apex predators, and hotter and drier climates (Ward-Jones et al., 2019; Wyborn, 2009). Each of these pose a significant threat of destabilisation to Kosciuszko NP's capacity to remove carrion from the landscape that now has a contextual background through the efforts of this research project.

Currently in the Australian Alps, feral ungulates are outpacing management actions to control their populations (Brown et al., 2016; Driscoll et al., 2019; Hall and Gill, 2005; Moriarty, 2004). This is exacerbated by Australia's lack of an endemic predator large and abundant enough to prey upon them and as a consequence their populations have expanded rapidly (Forsyth et al., 2019; Ward-Jones et al., 2019). The growth of ungulate populations along with the management actions to control them creates surges of carrion. This may overwhelm Kosciuszko NP's necrobiome as carcasses persist for long periods. This may have the unintended consequences of promoting exotic scavenging species such as red fox, feral cat, and the European wasp (Newsome et al., 2015; Read and Wilson, 2004; Spencer et al., 2020).

Climate change is altering Kosciuszko NP's environment (Wyborn, 2009) which may influence insect behaviour and distribution (Baz et al., 2007; De Jong and Chadwick, 1999). Because anthropogenic climate change may be all-encompassing, there are countless scenarios of fauna and flora responses. However, one simple scenario may be that rising temperatures within Kosciuszko NP may expand the temporal window in which insects are active. As seen in results from Chapter 1, carcass decay and insect activity are positively correlated with rising temperatures. Thus, future models of an optimal time for carrion decomposition may expand temporally with a similarly expanding warmer season. Although rising temperatures from anthropogenic climate change may not be a desired outcome from nearly any standpoint, it may promote decomposition by enabling insects to operate for a longer timeframe throughout the year.

Research Directions

This study has displayed the fragility of Kosciuszko NP's necrobiome and the limitations to its capacity to recycle carrion. This has sparked additional research questions directed at promoting the necrobiome and optimising decomposition. These future research directions can be asked in the following questions:

1) Do predator controls reduce vertebrate scavenger's capacity to consume carrion?
2) How can humans accelerate carcass decay?

The first question addresses if human actions to control predator canids influence vertebrate scavenger's contribution to carcass removal. Dingoes and red foxes, the primary targets of predator controls, are also some of the largest vertebrate scavengers in Australian ecosystems and possibly consume more carrion than other facultative scavengers (Spencer and Newsome, 2021). However, annual predator controls aimed at reducing dingo and red fox abundance due to agricultural and environmental impacts they cause may also disrupt their capacity to scavenge carcasses. Therefore, halting predator controls may have a positive response with vertebrate scavengers. What is not known yet is if that also has an impact on carcass persistence; in the absence of predator baiting do vertebrates contribute more to carrion removal and/or accelerate decay? This may be a cost-efficient way to promote efficient carcass removal, although any such actions would need to consider the potential negative impacts of red foxes on biodiversity more broadly.

The second question addresses anthropogenic means to accelerate carcass decay in place of a functional vertebrate scavenging guild. Without vertebrate scavengers to remove carrion, is there a way humans can compensate some of that functionality? This is important as it may identify a way in which humans can promote carrion recycling in the absence of a functional vertebrate guild and without changes to other animal controls. Large quantities of animals are culled by natural resource managers and agricultural practitioners and left in place to decompose. However, as seen through this study, these artificial surges of carrion are only efficiently processed in warmer months. Thus, there is a need to identify quick, cost-efficient methods humans can implement to reduce carcass persistence. This may identify cost-efficient actions humans can take to promote decomposition without compromising beneficial aspects of animal controls.

Information to Managers

As more stress is being placed on Kosciuszko NP's necrobiome to process carrion, managing carcass loads may be a necessity to sustain functional scavenger guilds. Although decomposition of carcasses is a natural process, the saying "too much of a good thing" may fit the scenario of Kosciuszko NP as an overabundance of carrion can have detrimental impacts such as unregulated nutrient release, disease persistence, or benefits to invasive species (Newsome et al., 2015; O'Bryan et al., 2018; Vicente and VerCauteren, 2019). Thus, maintaining a functional scavenger guild by promoting scavenging species and managing carcass loads may be necessary for the biodiversity of Kosciuszko NP. This is particularly relevant with the invasion of large feral ungulates that threaten biodiversity, and the current practices park managers choose to mitigate the threat (Hall and Gill, 2005; Ward-Jones et al., 2019). As it stands, feral animal culls for ungulates, felids, and canids are in operation annually and typically in autumn and winter (New South Wales et al., 2006) but efforts to identify impacts are limited.

Carcass decay throughout Kosciuszko NP's subalpine is accelerated by insect activity brought on by warmer temperatures. This study shows that carrion input during colder seasons will persist until temperatures rise and necrophagous insects can consume it. This is especially important to wildlife management as feral ungulate and canid removal programs occur in winter (March-April and May-June respectively) while its easiest to target breeding females (New South Wales et al., 2006). As many animals taken because of these management actions are left out in the environment, this study suggests that the carcasses will remain in a suspended state of decay until temperatures rise. Although this prolongs available nutrients to vertebrate scavengers, this also prolongs potential disease vectors (Vicente and VerCauteren, 2019). Carcasses may have diseases prior to their take which can possibly transfer to visiting vertebrates, thus a prolonged carcass decay may expose more vertebrates to carrion-born illnesses (Sage et al., 2019). Likewise, carcasses that have a longer window of availability to vertebrates can promote disease transmission between vertebrate scavengers (Markandya et al., 2008). Thus, animal controls in Kosciuszko NP during autumn and winter without consideration to carcass management may not be ideal timing for managing disease among wild animals.

In response to feral and pest animal management in winter, this study suggests the following adaptations to help manage carrion load in the environment and the negative effects that come with its excess:

1) **Cater control activity to suite ideal necrophagous insect activity**. This means changing the timing of large take operations to warmer months such as spring and summer (September-January).

2) **Remove excess carrion from the ecosystem when carrion recycling is at its slowest**. This means reducing the impact from artificially elevated carrion input by actively removing carcasses or preventing access by vertebrate scavengers.

3) **Promote a functional vertebrate scavenger guild**. This would recover lost functionality from anthropogenic disruption.

The simplest method to manage carrion in Kosciuszko NP may be to limit animal controls to the times when carrion recycling is optimises—namely the warm seasons of late-spring to early summer (Figure 36). During this time, insects are at their most active and able to quickly consume carrion thus shortening a window of disease transmission and ensuring nutrient dispersal. This would mean a change to a common practice of targeting pest animals during their winter breeding seasons. For ungulates especially this may be a large change as they form large groups for mating making them easier to target and control. However, a study of aerial-culling efficacy of feral deer in New Zealand showed that a change of aerial search patterns based on environmental variables yielded the greatest kill abundance and efficiency in summer (Latham et al., 2018). This suggests that aerial hunting during summer conditions may be a viable option as conditions for deer's detection in temperate forests by human spotters may be optimised. Theoretically, this approach would allow for Kosciuszko NP's ecosystem to efficiently decompose large quantities of carrion by operating within the bounds of its primary decomposer: necrophagous insects.

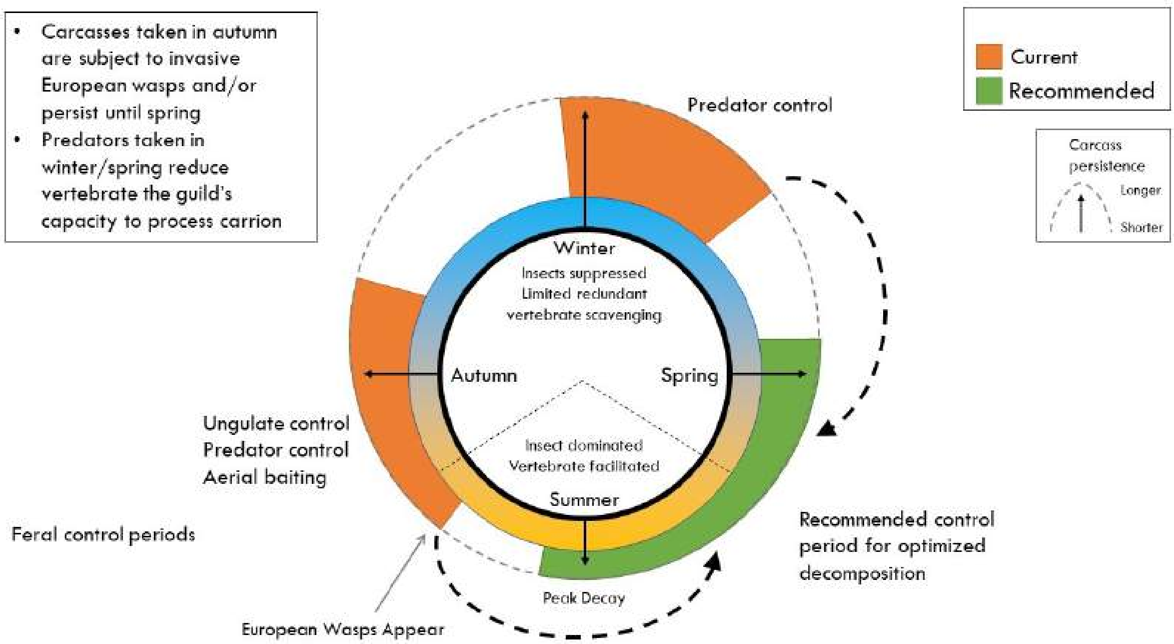


Figure 36: A conceptual diagram of Kosciuszko NP's scavenging regime with annotation of current feral animal controls and suggestions for improvement. Typically, in Kosciuszko NP, annual controls are conducted once in autumn and once in winter. Predator controls are usually implemented in winter. This is sub-optimal for carrion recycling as 1) carcasses that appear in the cold will persist until conditions warm and 2) vertebrate scavengers' capacity to remove carrion is reduced. This diagram suggests moving animal controls to accommodate insect scavengers by conducting management operations during

periods when insects are most active. This should result in much shorter carcass persistence and reducing the window of disease transmission.

Another solution to managing carcass input in Kosciuszko NP may be manually removing carrion from the environment. This could be realised by 1) a physical removal of the carcass from vertebrate scavengers with a disposal away from the susceptible environment, or 2) an exclusion of the carcass from vertebrate scavengers. The first method is conceptually simplistic but requires a large effort to both locate the carrion targeted in the culling then disposing it in a way vertebrate scavengers would be unable to interact with it. This method, if unproperly executed, may result an elevated risk of disease transmission from the carcass to humans. The second method employs an ecological "removal" of carrion by denying access to vertebrate scavengers that could potentially acquire disease from the carrion. This also would require an extensive effort and resources to mitigate vertebrate interactions but would reduce risk of disease exposure to humans. Both removal strategies would require an extensive effort that in some circumstances may not be practical.

The final method of mitigating a carrion load would be to bolster vertebrate scavenger guild either by 1) promoting established vertebrate scavengers or 2) introducing an apex scavenger historically native to the environment. The first strategy would mean promoting Kosciuszko NP's largest apex predator, the dingo, to utilise its ability to remove carrion. Dingoes are known scavengers that are capable of removing large quantities of carrion (Spencer and Newsome, 2021). However, predator controls active in Kosciuszko NP suppressing canids (including the dingo) may reduce their capacity to remove carrion. This disturbance to the vertebrate scavenger assemblage may have destabilised the community structure with no alternative scavenger that can efficiently recycle carrion (Huijbers et al., 2015). Therefore, efforts to promote the dingo may see a restoration in both the vertebrate assemblage and its ability to impact carrion (Wilson and Wolkovich, 2011). This first strategy means a halt in the management of predator controls and allowing vertebrates to re-establish a community structure. Alternatively, the second strategy seeks to fill the void left by the suppression of Kosciuszko NP's apex predator by introducing an apex scavenger, the Tasmanian Devil. From an ecology and evolutionary perspective, Tasmanian Devils are an apex scavenger capable of providing community structure around carrion (Cunningham et al., 2018) and has been historically present on the Australian mainland (Brown, 2006). In theory, the introduction of this apex scavenger to Kosicuszko NP may decrease carcass persistence as they consume carrion in large quantities. In a study of Tasmanian Devil scavenging dynamics, areas with greater abundance of Tasmanian Devils showed a shorter carcass persistence and less mesopredators than areas their absence which had longer carcass persistence and more mesopredators (Cunningham et al., 2018). The introduction of this apex scavenger may restructure Kosciuszko NP's necrobiome by supplementing or replacing other facultative vertebrate scavengers. However, this strategy is controversial as one reason being it may create unknown trophic effects on other endemic species. Both strategies (A: promote dingoes; B: introduce Tasmanian devils) to restore function to the vertebrate scavenger guild could be viable options that could effectively remove carrion. The first option may be preferable as it may be cost-efficient with less associated uncertainties.

Lastly, additional consideration should be considered in the timing of animal controls as invasive European wasps become active in late summer to early autumn. European wasp populations are increasing and excluding some insect and vertebrate scavengers access to carrion (Spencer et al., 2020). Providing an artificial increase of carrion while European wasps reach their peak activity during early Autumn could possibly promote wasp populations and fuel their exclusionary efforts. This provides a short window of opportunity for wildlife managers to optimally utilise endemic scavengers of Kosciuszko NP to process carrion and mitigate invasive wasps. To optimally use Kosciuszko NP's ability to recycle carrion without promoting invasive wasps, I suggest culling efforts between September through January (spring to early summer).

Conclusion

Scavenging, the process of organisms consuming deceased animal tissue, is present in every ecosystem (Benbow et al., 2015b). It is vital for recycling and dispersing nutrients throughout the environment as well as regulating disease transmission (Olea et al., 2019a). It is important to understand scavenging and how it fit into food-webs as it is an indicator for ecosystem health (Newsome et al., 2021). When scavenging is optimised, microbes, insects, and vertebrates operate in a structured way to efficiently recycle carrion (Barton and Bump, 2019; Wilson and Wolkovich, 2011).

Although Kosciuszko NP's scavenger assemblage contain a diversity of microbes, insects, and vertebrates, not all contribute evenly or efficiently to remove carrion thus creating a heavy reliance on one guild. Results from this study show, decomposition of animal tissue is optimised only during warmer seasons when insects are at their most active [see section "Chapter 1: Insects drive carrion decomposition in a temperate montane environment"]. Vertebrate scavengers fed on carcasses year-round, but they did not significantly impact decay. This was particularly apparent during cold seasons when vertebrates were the only scavenger guild capable of consuming carrion, yet decay rates did not differ between exclusion treatments. This makes Kosciuszko NP's ability to process carcasses heavily dependent on necrophagous insects.

The findings of this study provide insight for ecologists about the health of Kosciuszko NP's ecosystem (particularly its necrobiome) as well as suggestions to managers to maintain and indeed improve ecosystem functionality. The necrobiome is a rarely thought-of aspect of ecology yet it is ever present and vital in maintaining functional ecosystems; and as such, it must be cared for. The Australian Alps are a unique ecosystem that, unfortunately, is under threat of feral invasions and anthropogenic changes and may need human intervention to thrive. Although the thought of Kosciuszko NP's ecosystem being fragile may seem inconceivable, it is at risk. It is my hope that these findings and evidence-based suggestions help restore the ecological integrity of Kosciuszko NP.

References

Anderson, G.S., Barton, P.S., Archer, M., Wallace, J.R., 2019. Invertebrate Scavenging Communities, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 45–69. https://doi.org/10.1007/978-3-030-16501-7_3

Barton, P.S., Bump, J.K., 2019. Carrion Decomposition, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 101–124. https://doi.org/10.1007/978-3-030-16501-7_5

Barton, P.S., Cunningham, S.A., Lindenmayer, D.B., Manning, A.D., 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia 171, 761–772. https://doi.org/10.1007/s00442-012-2460-3

Barton, P.S., Evans, M.J., 2017. Insect biodiversity meets ecosystem function: differential effects of habitat and insects on carrion decomposition. Ecological Entomology 42, 364–374. https://doi.org/10.1111/een.12395

Barton, P.S., Evans, M.J., Pechal, J.L., Benbow, M.E., 2017. Necrophilous Insect Dynamics at Small Vertebrate Carrion in a Temperate Eucalypt Woodland. Journal of Medical Entomology 54, 964–973. https://doi.org/10.1093/jme/tjw242

Baz, A., Cifrián, B., Díaz-äranda, L.M., Martín-Vega, D., 2007. The distribution of adult blow-flies (Diptera: Calliphoridae) along an altitudinal gradient in Central Spain. Annales de la Société entomologique de France (N.S.) 43, 289–296. https://doi.org/10.1080/00379271.2007.10697524

Beasley, J.C., Olson, Z.H., Selva, N., DeVault, T.L., 2019. Ecological Functions of Vertebrate Scavenging, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 125–157. https://doi.org/10.1007/978-3-030-16501-7_6

Benbow, M.E., Pechal, J.L., Mohr, R.M., 2015a. Community and Landscape Ecology of Carrion, in: Carrion Ecology, Evolution, and Their Applications. CRC Press.

Benbow, M.E., Tomberlin, J.K., Tarone, A.M. (Eds.), 2015b. Carrion Ecology, Evolution, and Their Applications. CRC Press, Boca Raton. https://doi.org/10.1201/b18819

Bird, M.I., Hutley, L.B., Lawes, M.J., Lloyd, J., Luly, J.G., Ridd, P.V., Roberts, R.G., Ulm, S., Wurster, C.M., 2013. Humans, megafauna and environmental change in tropical Australia. Journal of Quaternary Science 28, 439–452. https://doi.org/10.1002/jqs.2639

Braack, L.E.O., 1987. Community dynamics of carrion-attendant arthropods in tropical african woodland. Oecologia 72, 402–409. https://doi.org/10.1007/BF00377571

Bradshaw, C.J.A., 2012. Little left to lose: deforestation and forest degradation in Australia since European colonization. Journal of Plant Ecology 5, 109–120. https://doi.org/10.1093/jpe/rtr038

Braithwaite, R.W., 1990. Australia's Unique Biota: Implications for Ecological Processes. Journal of Biogeography 17, 347–354. https://doi.org/10.2307/2845364

Brown, D., Thomas, E., Herbert, K., Primrose, K., 2016. Evaluating the effects of feral deer management on endangered alpine peatlands: The Alpine National Park deer control trial. Plant Protection Quarterly 31, 63.

Brown, O.J.F., 2006. Tasmanian devil (Sarcophilus harrisii) extinction on the Australian mainland in the mid-Holocene: multicausality and ENSO intensification. Alcheringa: An Australasian Journal of Palaeontology 30, 49–57. https://doi.org/10.1080/03115510609506855

Carter, D.O., Yellowlees, D., Tibbett, M., 2007. Cadaver decomposition in terrestrial ecosystems. Naturwissenschaften 94, 12–24. https://doi.org/10.1007/s00114-006-0159-1

Cook, D.E., 2021. Anthropogenic environmental change on the frontiers of European colonisation in Australia, A.D. 1788–1840. A reply to comments in Woodward (2020). Geomorphology 373, 107234. https://doi.org/10.1016/j.geomorph.2020.107234

Cook, D.E., 2019. Butzer 'Down Under': Debates on anthropogenic erosion in early Colonial Australia. Geomorphology 331, 160–174. https://doi.org/10.1016/j.geomorph.2018.12.011

Cunningham, C.X., Johnson, C.N., Barmuta, L.A., Hollings, T., Woehler, E.J., Jones, M.E., 2018. Top carnivore decline has cascading effects on scavengers and carrion persistence. Proceedings. Biological sciences 285. https://doi.org/10.1098/rspb.2018.1582

De Jong, G.D., Chadwick, J.W., 1999. Decomposition and Arthropod Succession on Exposed Rabbit Carrion During Summer at High Altitudes in Colorado, USA. J Med Entomol 36, 833–845. https://doi.org/10.1093/jmedent/36.6.833

DeVault, T.L., Brisbin, Jr., I.L., Rhodes, Jr., O.E., 2004. Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers. Can. J. Zool. 82, 502–509. https://doi.org/10.1139/z04-022

DeVault, T.L., Jr, O.E.R., Shivik, J.A., 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102, 225–234. https://doi.org/10.1034/j.1600-0706.2003.12378.x

DeVault, T.L., Rhodes, O.E., 2002. Identification of vertebrate scavengers of small mammal carcasses in a forested landscape. Acta Theriol 47, 185–192. https://doi.org/10.1007/BF03192458

Dickman, C.R., 1996. Impact of exotic generalist predators on the native fauna of Australia. wbio 2, 185–195. https://doi.org/10.2981/wlb.1996.018

Driscoll, D.A., Worboys, G.L., Allan, H., Banks, S.C., Beeton, N.J., Cherubin, R.C., Doherty, T.S., Finlayson, C.M., Green, K., Hartley, R., Hope, G., Johnson, C.N., Lintermans, M., Mackey, B., Paull, D.J., Pittock, J., Porfirio, L.L., Ritchie, E.G., Sato, C.F., Scheele, B.C., Slattery, D.A., Venn, S., Watson, D., Watson, M., Williams, R.M., 2019. Impacts of feral horses in the Australian Alps and evidence-based solutions. Ecological Management and Restoration 20, 63–72. https://doi.org/10.1111/emr.12357

Fillios, M., Gordon, C., Koch, F., Letnic, M., 2010. The effect of a top predator on kangaroo abundance in arid Australia and its implications for archaeological faunal assemblages. Journal of Archaeological Science 37, 986–993. https://doi.org/10.1016/j.jas.2009.11.031

Forsyth, D., Latham, A., Davis, N., Caley, P., Letnic, M., Moloney, P., Woodford, L., Woolnough, A., 2019. Interactions between dingoes and introduced wild ungulates: concepts, evidence and knowledge gaps. Australian Mammalogy 41, 12–26. https://doi.org/10.1071/AM17042

Gill, A.M., 1975. Fire and The Australian Flora: A Review. Australian Forestry 38, 4–25. https://doi.org/10.1080/00049158.1975.10675618

Hall, G.P., Gill, K.P., 2005. Management of Wild Deer in Australia. The Journal of Wildlife Management 69, 837–844. https://doi.org/10.2193/0022-541X(2005)069[0837:MOWDIA]2.0.CO;2

Hill, J.E., DeVault, T.L., Beasley, J.C., Rhodes, O.E., Belant, J.L., 2018. Effects of vulture exclusion on carrion consumption by facultative scavengers. Ecology and Evolution 8, 2518–2526. https://doi.org/10.1002/ece3.3840

Houston, D.C., 1985. Evolutionary Ecology of Afrotropical and Neotropical Vultures in Forests. Ornithological Monographs 856–864. https://doi.org/10.2307/40168321

Huijbers, C.M., Schlacher, T.A., Schoeman, D.S., Olds, A.D., Weston, M.A., Connolly, R.M., 2015. Limited functional redundancy in vertebrate scavenger guilds fails to compensate for the loss of raptors from urbanized sandy beaches. Diversity and Distributions 21, 55–63. https://doi.org/10.1111/ddi.12282

Latham, A.D.M., Cecilia Latham, M., Herries, D., Barron, M., Cruz, J., Anderson, D.P., 2018. Assessing the efficacy of aerial culling of introduced wild deer in New Zealand with analytical decomposition of predation risk. Biol Invasions 20, 251–266. https://doi.org/10.1007/s10530-017-1531-0

Lawrence, S., Davies, P., 2011. An Archaeology of Australia Since 1788, Contributions To Global Historical Archaeology. Springer New York, New York, NY. https://doi.org/10.1007/978-1-4419-7485-3

Markandya, A., Taylor, T., Longo, A., Murty, M.N., Murty, S., Dhavala, K., 2008. Counting the cost of vulture decline—An appraisal of the human health and other benefits of vultures in India. Ecological Economics, Special Section: Biodiversity and Policy 67, 194–204. https://doi.org/10.1016/j.ecolecon.2008.04.020

Moleón, M., Sánchez-Zapata, J.A., Sebastián-González, E., Owen-Smith, N., 2015. Carcass size shapes the structure and functioning of an African scavenging assemblage. Oikos 124, 1391–1403. https://doi.org/10.1111/oik.02222

Moleón, M., Selva, N., Quaggiotto, M.M., Bailey, D.M., Cortés-Avizanda, A., DeVault, T.L., 2019. Carrion Availability in Space and Time, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 23–44. https://doi.org/10.1007/978-3-030-16501-7_2

Moriarty, A., 2004. The liberation, distribution, abundance and management of wild deer in Australia. Wildl. Res. 31, 291. https://doi.org/10.1071/WR02100

Munoz-Lozano, C., Martin-Vega, D., Martinez-Carrasco, C., Sanchez-Zapata, J.A., Morales-Reyes, Z., Gonzalvez, M., Moleon, M., 2019. Avoidance of carnivore carcasses by vertebrate scavengers enables colonization by a diverse community of carrion insects. PLoS One 14, e0221890. https://doi.org/10.1371/journal.pone.0221890

New South Wales, Department of Environment and Conservation, Parks and Wildlife Division, New South Wales, Department of Environment and Conservation, 2006. Kosciuszko National Park plan of management: 2006. Dept. of Environment and Conservation NSW, Sydney South, N.S.W.

Newsome, A., 1990. The control of vertebrate pests by vertebrate predators. Trends in Ecology & Evolution 5, 187–191. https://doi.org/10.1016/0169-5347(90)90208-U

Newsome, T.M., Barton, B., Buck, J.C., DeBruyn, J., Spencer, E., Ripple, W.J., Barton, P.S., 2021. Monitoring the dead as an ecosystem indicator. Ecology and Evolution 11, 5844–5856. https://doi.org/10.1002/ece3.7542

Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A.J., Dickman, C.R., 2015. The ecological effects of providing resource subsidies to predators. Global Ecology and Biogeography 24, 1–11. https://doi.org/10.1111/geb.12236

O'Bryan, C.J., Braczkowski, A.R., Beyer, H.L., Carter, N.H., Watson, J.E.M., McDonald-Madden, E., 2018. The contribution of predators and scavengers to human well-being. Nat Ecol Evol 2, 229–236. https://doi.org/10.1038/s41559-017-0421-2

Ogada, D.L., Torchin, M.E., Kinnaird, M.F., Ezenwa, V.O., 2012. Effects of Vulture Declines on Facultative Scavengers and Potential Implications for Mammalian Disease Transmission: *Vulture Declines, Facultative Scavengers, and Disease Transmission*. Conservation Biology 26, 453–460. https://doi.org/10.1111/j.1523-1739.2012.01827.x

Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A., 2019a. Introduction to the Topic of Carrion Ecology and Management, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, José Antonio (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 1–20. https://doi.org/10.1007/978-3-030-16501-7_1

Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), 2019b. Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-030-16501-7

Orians, G.H., Milewski, A.V., 2007. Ecology of Australia: the effects of nutrient-poor soils and intense fires. Biological Reviews 82, 393–423. https://doi.org/10.1111/j.1469-185X.2007.00017.x

Payne, J.A., 1965. A Summer Carrion Study of the Baby Pig Sus Scrofa Linnaeus. Ecology 46, 592–602. https://doi.org/10.2307/1934999

Pechal, J.L., Benbow, M.E., Crippen, T.L., Tarone, A.M., Tomberlin, J.K., 2014. Delayed insect access alters carrion decomposition and necrophagous insect community assembly. ECOSPHERE 5. https://doi.org/10.1890/ES14-00022.1

Peers, M.J.L., Konkolics, S.M., Lamb, C.T., Majchrzak, Y.N., Menzies, A.K., Studd, E.K., Boonstra, R., Kenney, A.J., Krebs, C.J., Martinig, A.R., McCulloch, B., Silva, J., Garland, L., Boutin, S., 2020. Prey availability and ambient temperature influence carrion persistence in the boreal forest. Journal of Animal Ecology n/a. https://doi.org/10.1111/1365-2656.13275

Ray, R.-R., H. Seibold, M. Heurich, 2014. Invertebrates outcompete vertebrate facultative scavengers in simulated lynx kills in the Bavarian Forest National Park, Germany. Animal biodiversity and conservation 37.

Read, J.L., Wilson, D., 2004. Scavengers and detritivores of kangaroo harvest offcuts in arid Australia. Wildl. Res. 31, 51. https://doi.org/10.1071/WR02051

Sage, M.J.L., Towey, B.D., Brunner, J.L., 2019. Do scavengers prevent or promote disease transmission? The effect of invertebrate scavenging on Ranavirus transmission. Functional Ecology 33, 1342–1350. https://doi.org/10.1111/1365-2435.13335

Sebastián-González, E., Barbosa, J.M., Pérez-García, J.M., Morales-Reyes, Z., Botella, F., Olea, P.P., Mateo-Tomás, P., Moleón, M., Hiraldo, F., Arrondo, E., Donázar, J.A., Cortés-Avizanda, A., Selva, N., Lambertucci, S.A., Bhattacharjee, A., Brewer, A., Anadón, J.D., Abernethy, E., Rhodes, O.E., Turner, K., Beasley, J.C., DeVault, T.L., Ordiz, A., Wikenros, C., Zimmermann, B., Wabakken, P., Wilmers, C.C., Smith, J.A., Kendall, C.J., Ogada, D., Buechley, E.R., Frehner, E., Allen, M.L., Wittmer, H.U., Butler, J.R.A., du Toit, J.T., Read, J., Wilson, D., Jerina, K., Krofel, M., Kostecke, R., Inger, R., Samson, A., Naves-Alegre, L., Sánchez-Zapata, J.A., 2019. Scavenging in the Anthropocene: Human impact drives vertebrate scavenger species richness at a global scale. Global Change Biology 3005–3017. https://doi.org/10.1111/gcb.14708

Sebastián-González, E., Moleon, M., Gibert, J., Botella, F., Mateo-Tomas, P., Olea, P., Guimaraes, P., Sanchez-Zapata, J., 2016. Nested species-rich networks of scavenging vertebrates support high levels of interspecific competition. Ecology 97, 95–105. https://doi.org/10.1890/15-0212.1

Smith, J.B., Laatsch, L.J., Beasley, J.C., 2017. Spatial complexity of carcass location influences vertebrate scavenger efficiency and species composition. Sci Rep 7, 10250. https://doi.org/10.1038/s41598-017-10046-1

Spencer, E., Newsome, T., 2021. Dingoes dining with death. Australian Zoologist 41, 433–451. https://doi.org/10.7882/AZ.2021.008

Spencer, E.E., Barton, P.S., Ripple, W.J., Newsome, T.M., 2020. Invasive European wasps alter scavenging dynamics around carrion. Food Webs 24, e00144. https://doi.org/10.1016/j.fooweb.2020.e00144

van Eeden, L.M., Smith, B.P., Crowther, M.S., Dickman, C.R., Newsome, T.M., 2019. 'The dingo menace': an historic survey on graziers' management of an Australian carnivore. Pac. Conserv. Biol. 25, 245. https://doi.org/10.1071/PC18031

Vicente, J., VerCauteren, K., 2019. The Role of Scavenging in Disease Dynamics, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 161–182. https://doi.org/10.1007/978-3-030-16501-7_7

Ward-Jones, J., Pulsford, I., Thackway, R., Bishwokarma, D., Freudenberger, D., 2019. Impacts of feral horses and deer on an endangered woodland of Kosciuszko National Park. Ecological Management & Restoration 20, 37–46. https://doi.org/10.1111/emr.12353

Wilson, E.E., Wolkovich, E.M., 2011. Scavenging: How carnivores and carrion structure communities. Trends in Ecology and Evolution 26, 129–135. https://doi.org/10.1016/j.tree.2010.12.011

Woinarski, J.C.Z., Braby, M.F., Burbidge, A.A., Coates, D., Garnett, S.T., Fensham, R.J., Legge, S.M., McKenzie, N.L., Silcock, J.L., Murphy, B.P., 2019. Reading the black book: The number, timing, distribution and causes of listed extinctions in Australia. Biological Conservation 239, 108261. https://doi.org/10.1016/j.biocon.2019.108261

Wyborn, C., 2009. Managing change or changing management: climate change and human use in Kosciuszko National Park. Australasian Journal of Environmental Management 16, 208–217. https://doi.org/10.1080/14486563.2009.9725236

Appendix

Appendix

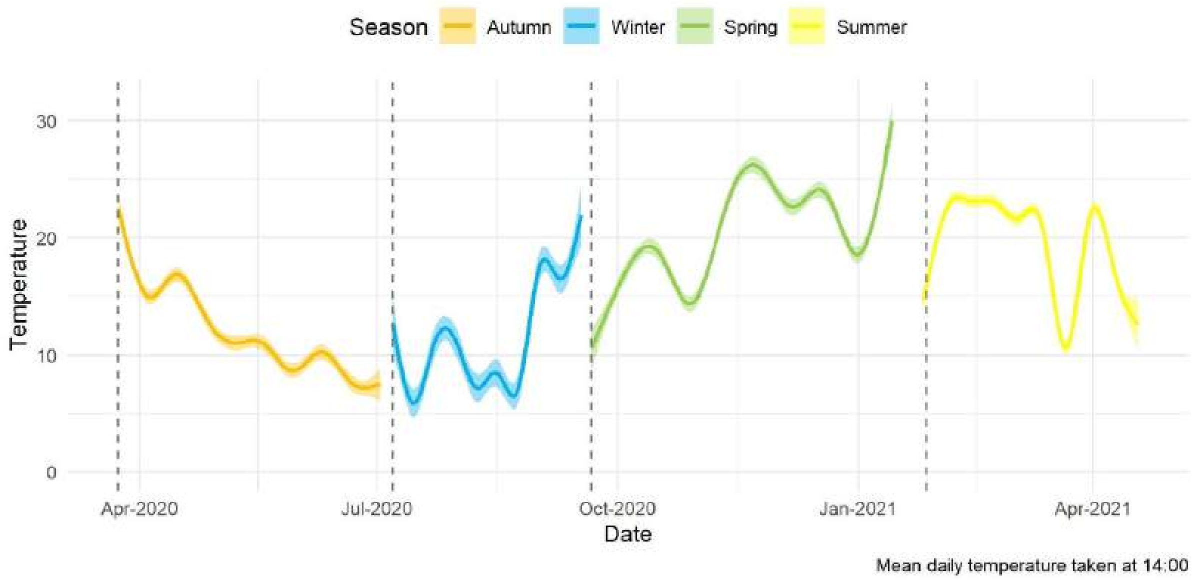
Chapter 1

The following are figures and tables used in the analysis of "Chapter 1: Insects drive carrion decomposition in a temperate montane environment".

Appendix 1: The number of carcass treatments in each seasonal replicate reaching decomposition stage or biomass marker.

Season	Treatment	Stage			Mass	
		Active	Advanced	Dry	50%	10%
Autumn	Open	7	3	1	5	3
	Cage	7	0	0	4	0
	Cage, mesh	3	0	0	1	0
Winter	Open	5	2	1	2	0
	Cage	8	3	0	5	0
	Cage, mesh					
Spring	Open	8	8	8	8	8
	Cage	8	8	7	8	7
	Cage, mesh	8	8	4	8	2
Summer	Open	8	8	8	8	8
	Cage	8	8	8	8	8
	Cage, mesh	8	8	8	8	8

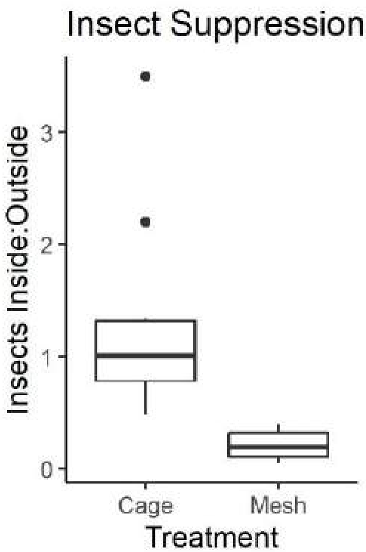
Appendix 2: Mean daily max temperatures during the study. Temperatures were collected daily by Reconyx PC800 Hyperfire™ cameras at 14:00 from all treatments. Temperatures were compiled and a generalised additive model with smoothness was applied. Grey vertical lines mark carcass deployment for the preceding replicate.



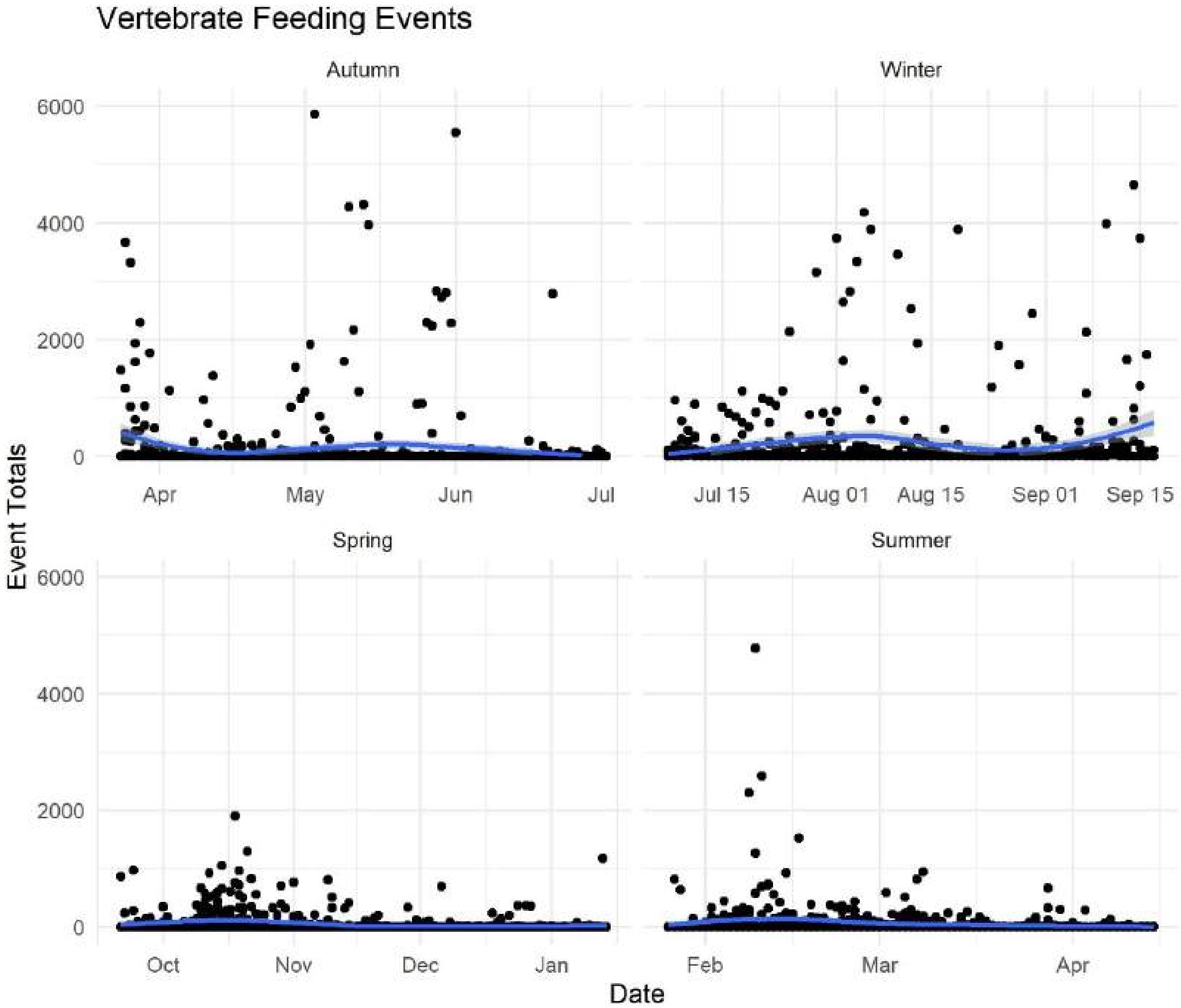
Appendix 3: Total counts of insect taxa collected during the first three days of monitoring carcass decay. The total count of ants, beetles, flies, wasps, and other insects for all seasons is 8,248.

Season	Exclusion	Ant	Beetle	Fly	Wasp	Other
Autumn	Open	2,090	145	79	200	69
	Vertebrate	3,683	137	122	170	42
Winter	Open	7	49	6	0	121
	Vertebrate	6	39	11	1	100
Spring	Open	81	74	63	0	35
	Vertebrate	74	74	55	0	71
Summer	Open	266	19	30	0	33
	Vertebrate	171	44	66	0	15

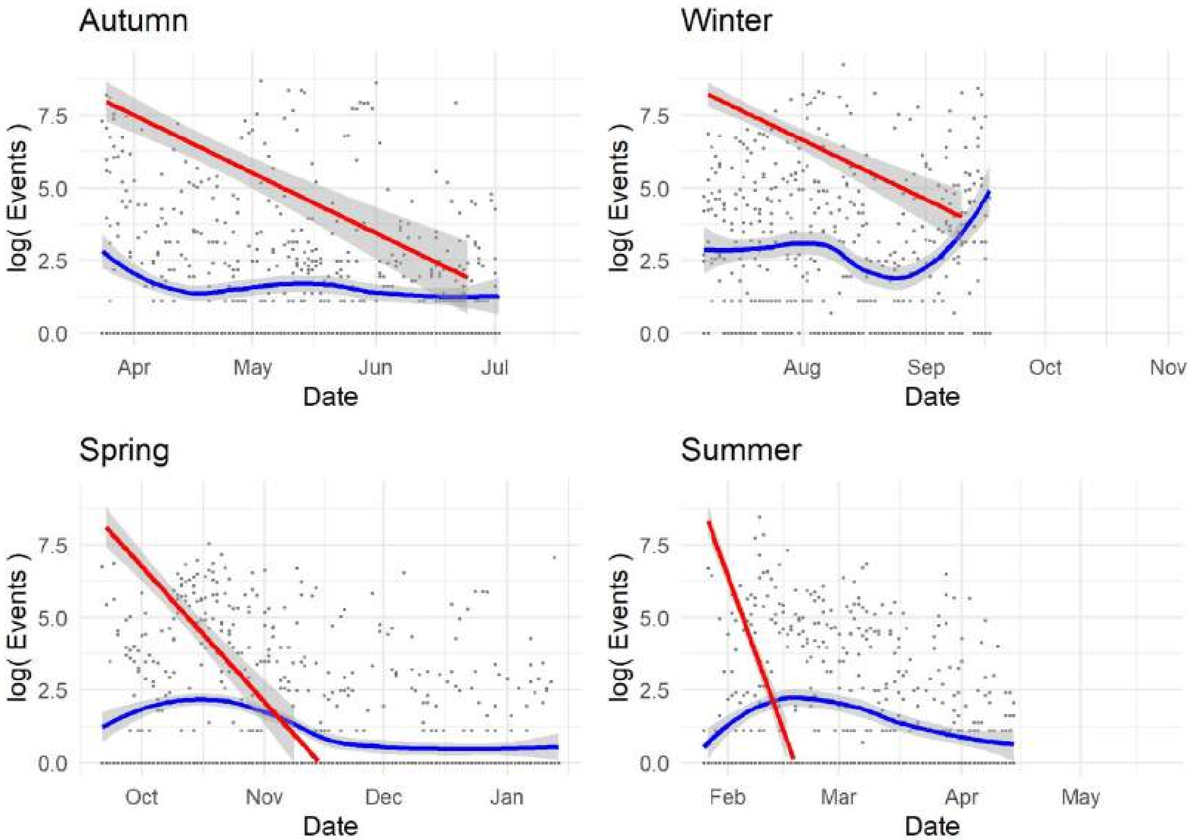
Appendix 4: Ratio of insects collected from inner to outer traps at vertebrate exclusion and insect suppression cage treatments from the first 72 hours of carcass monitoring. A Kruskal-Wallis one-way analysis of variance was performed (χ^2_{KW-H} = 17.778 on 1 df, p = 2.5e-05) suggesting a suppression effect from the insect mesh on the insect suppression treatments.



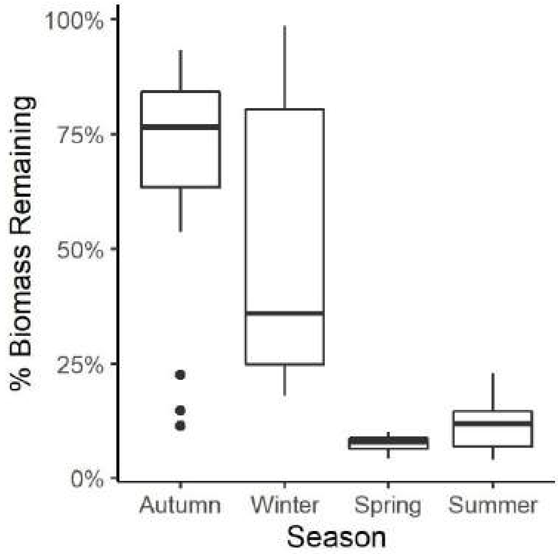
Appendix 5: Vertebrate feeding events tallied for each day of monitoring. Colder seasons of autumn and summer recorded the highest feeding activity. Feeding activity appears to peak earlier in warmer seasons



Appendix 6: Vertebrate feeding events (log scaled) and biomass recorded in each seasonal replicate. Vertebrate events were tallied and scaled then a localised regression model (Blue) was applied. A linear regression of carcass biomass (Red) from all treatments was overlayed on top. Biomass estimates were taken from time lapse imagery. Decay was fastest in summer which also had the lowest amount of vertebrate activity. Carcasses during that time were consumed quickly by scavenging insects possibly outcompeting vertebrates. Winter had the slowest decay, but also the most vertebrate events. The slower decay may have prolonged the window of availability to vertebrate scavengers. Insect activity on the winter carcasses was suppressed due to the low temperatures but rapidly increased with the warmer temperatures brought on by seasonal change. The thawing carcasses and increased insect activity may have produced cues vertebrate scavengers could use which may explain the sudden increase of vertebrate activity towards the end of the replicate.



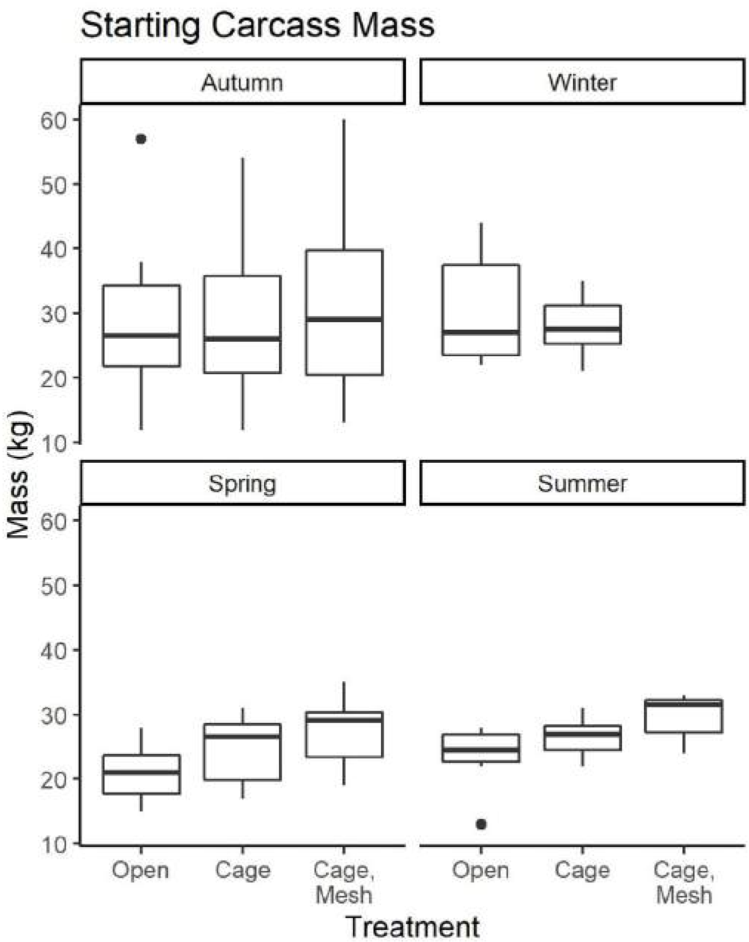
Appendix 7: Carcass biomass remaining as measured from the deployment to the completion of each replicate. Mass is scaled to percentage to compare between replicates.



Appendix 8: Mean carcass biomass remaining at each replicate.

Season	μ	σ
Autumn	69%	23%
Winter	51%	31%
Spring	8%	2%
Summer	12%	6%

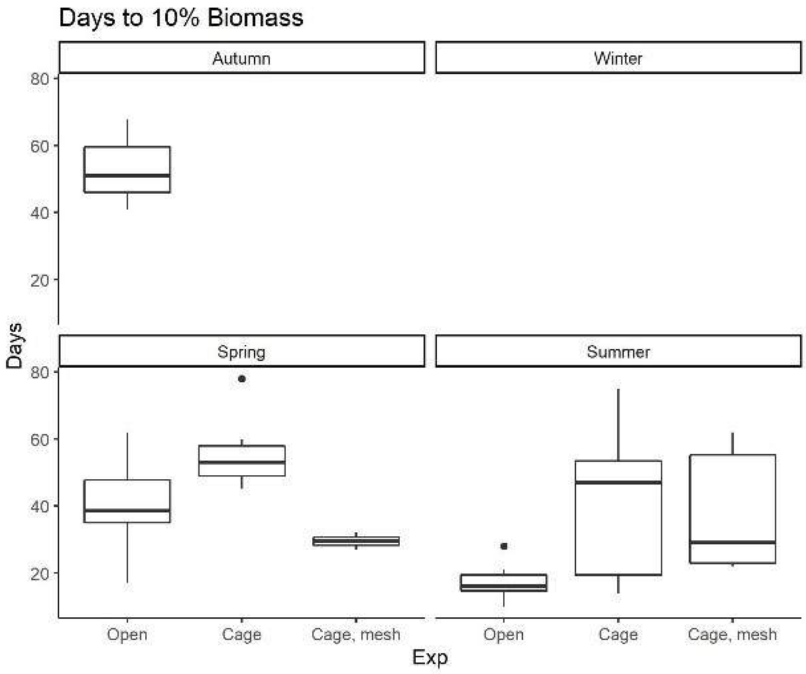
Appendix 9: Mean starting carcass biomass for each treatment and season.



Appendix 10: Mean starting carcass mass in kilograms of each seasonal replicate and treatment.

Season	Exclusion	μ (kg)	σ	σ^2
Autumn	Open	29.5	13.6	184.9
	Vertebrate	30.0	14.8	218.9
	Vertebrate + Insect	32.5	17.5	307.7
Winter	Open	30.3	8.5	72.8
	Vertebrate	28.1	5.1	25.6
	Vertebrate + Insect			
Spring	Open	21.0	4.9	23.9
	Vertebrate	24.7	5.2	26.7
	Vertebrate + Insect	27.2	5.6	31.1
Summer	Open	23.6	4.8	22.8
	Vertebrate	26.5	3.0	9.1
	Vertebrate + Insect	29.8	3.6	13.1

Appendix 11: A boxplot of the number of days at which carcasses reached 10% biomass across treatments and faceted by season. Autumn and winter had 2 and 0 carcasses reach this stage creating an imbalance in an analysis of variance result.



	Collection Period					
Season	0-3	3-6	6-9	9-12	12-15	Complication
Autumn	✓	✓	✓			COVID-19
Winter	✓					Snowstorm
Spring	✓	✓	½	½		Snowstorm
Summer	✓	✓	✓	✓	✓	None

Appendix 12: A visual representation of the insect collection periods for each seasonal replicate and their success. This project's original necrophilous insect sampling scheme for each replicate was five collection periods (duration 3-days) for the first fifteen days of carcass deployment. However, due to circumstances beyond this project's control, the Autumn, Winter, and Spring replicates suffered from a lack of access from inclement weather and the University of Sydney's response to the COVID-19 pandemic. The Autumn field season in April of 2020 was terminated prematurely due to the lockdown and travel restrictions imposed by the New South Wales Government and the University of Sydney. Consequently, field collections for insects concluded at day 9 of decomposition as the field team was required to return to the University campus. The Winter and Spring replicates suffered from large snowstorms that physically blocked access to the carcass sites. In addition, the National Parks and Wildlife Service restricted access during major storms for safety precautions and protection of dirt-road access ways. This restricted collections for the winter treatment to just the first three days. For Spring, several storms delayed carcass deployment to half of the transect for several days. The result being half of the sites were accessible for twelve days while the other were accessible for only six. Summer had no complications due to access but did a large precipitation event during the first collection period (days 0-3) which can be seen in the extreme drop in temperature relative to the mean summer temperatures (Appendix 2; Appendix 30).

Chapter 2

The following are figures and tables used in the analysis of "Chapter 2: Necrophilous insect responses to the experimental restriction of facultative vertebrate scavengers".

Appendix 13: Count of insect taxa collected at carcasses during collection periods

Taxa	Collection Round					
	0-3	3-6	6-9	9-12	12-15	Total
Ant	437 (3.3%)	533 (4.0%)	381 (2.9%)	340 (2.6%)	580 (4.4%)	2,271 (17.2%)
Beetle	63 (0.5%)	1,462 (11.1%)	2694 (20.4%)	1,300 (9.8%)	1,880 (14.2%)	7,399 (56.0%)
Fly	96 (0.7%)	1,461 (11.1%)	879 (6.7%)	259 (2.0%)	848 (6.4%)	3,543 (26.8%)
Collection	596 (4.5%)	3,456 (26.2%)	3,954 (29.9%)	1,899 (14.4%)	3,308 (25%)	13,213 (100.0%)

Appendix 14: A model selection table for community response to experimental exclusion of vertebrates in a multivariate analysis. Three models were competitive but neither model with temperature or elevation had significance and therefore were not chosen.

Model	k	AIC	AICc	ΔAICc
Community ~ Treatment + Day	6	192.60	193.75	0.00
Community ~ Treatment + Day + Temperature	7	193.47	195.02	1.27
Community ~ Treatment + Day + Elevation	7	193.51	195.06	1.32
Community ~ Treatment + Day + Temperature + Day:Temperature	11	192.24	196.12	2.37
Community ~ Treatment + Day + Temperature + Elevation	8	194.89	196.92	3.17
Community ~ Treatment + Day + Temperature + Elevation + Temperature:Elevation	9	195.20	197.77	4.02
Community ~ Treatment + Day + Temperature + Elevation + Day:Temperature	12	193.89	198.54	4.80
Community ~ Treatment + Day + Temperature + Elevation + Day:Temperature + Temperature:Elevation	13	195.29	200.80	7.06
Community ~ Treatment + Temperature	3	206.12	206.44	12.69
Community ~ Treatment + Temperature + Elevation	4	206.62	207.15	13.40
Community ~ Treatment + Temperature + Elevation + Temperature:Elevation	5	207.30	208.11	14.36
Community ~ Treatment	2	219.88	220.04	26.29
Community ~ Treatment + Elevation	3	221.18	221.50	27.75

Appendix 15: Model results from PERMANOVA of necrophagous insect community response to experimental treatments and time.

Variable	df	Sums Of Squares	Mean Squares	F	R2	Pr(>F)
Treatment	1	0.191	0.191	1.478	0.013	0.180
Day	4	5.299	1.325	10.256	0.352	0.001
Residuals	74	9.559	0.129		0.635	
Total	79	15.049			1.000	

Appendix 16: A model selection table and AIC for GLMMs of ant, beetle, and fly abundance in response to experimental treatments and permutations of variables.

Taxa	Model	K	AICc	ΔAICc
Ant	Abundance ~ Treatment + (1 | Site)	4	695.87	0.00
	Abundance ~ Treatment + Time + (1 | Site)	5	698.03	2.16
	Abundance ~ Treatment + Temperature + (1 | Site)	5	698.13	2.26
	Abundance ~ Treatment + Temperature + Elevation + Temperature:Elevation + (1 | Site)	7	698.71	2.84
	Abundance ~ Treatment + Time + Temperature + Elevation + (1 | Site)	7	699.92	4.05
	Abundance ~ Treatment + Time + Temperature + (1 | Site)	6	700.28	4.41
	Abundance ~ Treatment + Time + Temperature + Time:Temperature + (1 | Site)	7	700.60	4.73
	Abundance ~ Treatment + Time + Temperature + Elevation + Temperature:Elevation + (1 | Site)	8	701.18	5.31
	Abundance ~ Treatment + Time + Temperature + Elevation + Time:Temperature + Temperature:Elevation + (1 | Site)	9	701.34	5.46

Beetle	Abundance ~ Treatment + Time + Temperature + Time:Temperature + (1 | Site)	7	813.26	0.00
	Abundance ~ Treatment + Time + Temperature + Elevation + Time:Temperature + (1 | Site)	8	813.95	0.69
	Abundance ~ Treatment + Time + Temperature + Elevation + Time:Temperature + Temperature:Elevation + (1 | Site)	9	816.11	2.85
	Abundance ~ Treatment + Temperature + (1 | Site)	5	871.93	58.67
	Abundance ~ Treatment + Time + Temperature + (1 | Site)	6	873.78	60.52
	Abundance ~ Treatment + Temperature + Elevation + (1 | Site)	6	874.13	60.87
	Abundance ~ Treatment + Time + Temperature + Elevation + (1 | Site)	7	876.15	62.89
	Abundance ~ Treatment + Temperature + Elevation + Temperature:Elevation + (1 | Site)	7	876.37	63.11
	Abundance ~ Treatment + Time + Temperature + Elevation + Temperature:Elevation + (1 | Site)	8	878.42	65.16
	Abundance ~ Treatment + Time + (1 | Site)	5	880.70	67.44
	Abundance ~ Treatment + Time + Elevation + (1 | Site)	6	882.46	69.20
	Abundance ~ Treatment + (1 | Site)	4	890.76	77.50
	Abundance ~ Treatment + Elevation + (1 | Site)	5	892.55	79.29
Fly	Abundance ~ Treatment + Time + Temperature + Time:Temperature + (1 | Site)	7	741.76	0.00
	Abundance ~ Treatment + Time + Temperature + Elevation + Time:Temperature + (1 | Site)	8	743.31	1.55
	Abundance ~ Treatment + Time + Temperature + Elevation + Time:Temperature + Temperature:Elevation + (1 | Site)	9	745.23	3.46

`Abundance ~ Treatment + Temperature + (1 | Site)`	5	766.99	25.23
`Abundance ~ Treatment + (1 | Site)`	4	767.62	25.85
`Abundance ~ Treatment + Temperature + Elevation + (1 | Site)`	6	769.29	27.53
`Abundance ~ Treatment + Elevation + (1 | Site)`	5	769.55	27.79
`Abundance ~ Treatment + Time + (1 | Site)`	5	769.56	27.80
`Abundance ~ Treatment + Time + Elevation + (1 | Site)`	6	771.59	29.83
`Abundance ~ Treatment + Temperature + Elevation + Temperature:Elevation + (1 | Site)`	7	771.63	29.87
`Abundance ~ Treatment + Time + Temperature + Elevation + Temperature:Elevation + (1 | Site)`	8	772.77	31.01

Appendix 17: GLMM results from three separate models performed on ant, beetle, and fly abundancies in response to experimental treatment and select variables. Significance is denoted via asterisk with exception of the slope intercept.

Model	Variable	β	2.5%	97.5 %	se	z	*p*	sig.
Ant	*(Intercept)*	3.437	3.0	3.9	0.247	13.928	4.3E-44	
	Treatment	-0.530	-1.0	-0.1	0.234	-2.262	0.024	**
Beetle	*(Intercept)*	4.964	4.7	5.2	0.135	36.806	1.5E-296	
	Treatment	-0.198	-0.5	0.1	0.167	-1.185	0.236	
	Time	0.463	0.1	0.8	0.177	2.608	0.009	***
	Temperature	0.435	0.1	0.8	0.181	2.403	0.016	**
	Time × Temperature	-0.950	-1.1	-0.8	0.096	-9.930	3.1E-23	***
Fly	*(Intercept)*	4.184	3.8	4.6	0.219	19.130	1.4E-81	
	Treatment	0.054	-0.5	0.6	0.260	0.206	0.837	
	Time	0.201	-0.3	0.7	0.259	0.777	0.437	
	Temperature	0.137	-0.4	0.7	0.292	0.468	0.640	
	Time × Temperature	-0.866	-1.1	-0.6	0.142	-6.105	1.0E-09	***

Appendix 18: A model selection table of large and small beetle abundancies in response to experimental and permutations of environmental variables.

Model	K	AICc	ΔAICc
Abundance ~ Treatment + Time + Temperature + Taxa + Time:Temperature + (1 | Site)	8	1423.17	0.00
Abundance ~ Treatment + Time + Temperature + Elevation + Taxa + Time:Temperature + (1 | Site)	9	1423.19	0.02
Abundance ~ Taxa + Treatment + Time + Temperature + Time:Temperature + Taxa:Time + Taxa:Temperature + (1 | Site)	10	1423.62	0.46
Abundance ~ Treatment + Time + Temperature + Elevation + Taxa + Time:Temperature + Temperature:Elevation + (1 | Site)	10	1424.86	1.70
Abundance ~ Taxa + Treatment + Time + Temperature + Elevation + Time:Temperature + Temperature:Elevation + Taxa:Time + Taxa:Temperature + (1 | Site)	12	1425.45	2.28
Abundance ~ Taxa + Treatment + Time + Elevation + Time:Temperature + Temperature:Elevation + Taxa:Time + (1 | Site)	10	1429.12	5.95
Abundance ~ Taxa + Treatment + Temperature + Elevation + Time:Temperature + Temperature:Elevation + Taxa:Temperature + (1 | Site)	10	1435.19	12.03
Abundance ~ Treatment + Temperature + Taxa + (1 | Site)	6	1513.78	90.61
Abundance ~ Treatment + Time + Temperature + Taxa + (1 | Site)	7	1515.06	91.89
Abundance ~ Treatment + Temperature + Elevation + Taxa + (1 | Site)	7	1515.80	92.63
Abundance ~ Taxa + Treatment + Temperature + Taxa:Temperature + (1 | Site)	7	1515.82	92.66
Abundance ~ Treatment + Time + Temperature + Elevation + Taxa + (1 | Site)	8	1517.26	94.09
Abundance ~ Treatment + Temperature + Elevation + Taxa + Temperature:Elevation + (1 | Site)	8	1517.80	94.63
Abundance ~ Taxa + Treatment + Time + Temperature + Taxa:Time + Taxa:Temperature + (1 | Site)	9	1518.05	94.89
Abundance ~ Treatment + Time + Temperature + Elevation + Taxa + Temperature:Elevation + (1 | Site)	9	1519.23	96.07
Abundance ~ Treatment + Time + Taxa + (1 | Site)	6	1527.85	104.69
Abundance ~ Taxa + Treatment + Time + Taxa:Time + (1 | Site)	7	1528.53	105.37

Abundance ~ Treatment + Time + Elevation + Taxa + (1 | Site)	7	1528.84	105.68
Abundance ~ Treatment + Taxa + (1 | Site)	5	1547.27	124.10
Abundance ~ Treatment + Elevation + Taxa + (1 | Site)	6	1548.52	125.35

Appendix 19: GLMM model results of large- and small-sized beetle abundancies response to experimental treatment and associated variables.

Variable	β	2.5 %	97.5 %	SE	z	p	sig.
(Intercept)	4.250	4.0	4.5	0.132	32.224	8.0E-228	
Treatment	-0.205	-0.5	0.1	0.142	-1.444	0.149	
Time	0.456	0.2	0.8	0.151	3.026	0.002	**
Temperature	0.430	0.1	0.7	0.155	2.775	0.006	**
Taxa	0.047	-0.2	0.3	0.142	0.333	0.739	
Time × Temperature	-0.944	-1.1	-0.8	0.083	-11.349	7.53E-30	***

Appendix 20: A model selection table for abundance of two beetle species, Creophilus erythrocephalus (predator) and Ptomophila lacrymosa (scavenger) and their response to experimental treatment with permutations of abiotic variables.

Model	K	AICc	ΔAICc
Abundance ~ Taxa + Treatment + Time + Temperature + Time:Temperature + Taxa:Time + Taxa:Temperature + (1 | Site)	10	1067.04	0.00
Abundance ~ Taxa + Treatment + Time + Temperature + Elevation + Time:Temperature + Temperature:Elevation + Taxa:Time + Taxa:Temperature + (1 | Site)	12	1068.28	1.24
Abundance ~ Treatment + Time + Temperature + Taxa + (1 | Site) + Time:Temperature	8	1068.46	1.42
Abundance ~ Taxa + Treatment + Time + Elevation + Time:Temperature + Temperature:Elevation + Taxa:Time + (1 | Site)	10	1069.95	2.92
Abundance ~ Treatment + Time + Temperature + Elevation + Taxa + (1 | Site) + Time:Temperature	9	1070.27	3.23
Abundance ~ Treatment + Time + Temperature + Elevation + Taxa + (1 | Site) + Time:Temperature + Temperature:Elevation	10	1070.59	3.56
Abundance ~ Taxa + Treatment + Temperature + Elevation + Time:Temperature + Temperature:Elevation + Taxa:Temperature + (1 | Site)	10	1071.88	4.84

<table>
<tr><th></th><th></th><th></th><th></th></tr>
<tr><td>Abundance ~ Treatment + Temperature + Taxa + (1 | Site)</td><td>6</td><td>1161.56</td><td>94.52</td></tr>
<tr><td>Abundance ~ Treatment + Temperature + Elevation + Taxa + (1 | Site)</td><td>7</td><td>1162.73</td><td>95.70</td></tr>
<tr><td>Abundance ~ Treatment + Temperature + Elevation + Taxa + (1 | Site) + Temperature:Elevation</td><td>8</td><td>1163.06</td><td>96.02</td></tr>
<tr><td>Abundance ~ Taxa + Treatment + Temperature + Taxa:Temperature + (1 | Site)</td><td>7</td><td>1163.74</td><td>96.70</td></tr>
<tr><td>Abundance ~ Treatment + Time + Temperature + Taxa + (1 | Site)</td><td>7</td><td>1163.75</td><td>96.71</td></tr>
<tr><td>Abundance ~ Treatment + Time + Temperature + Elevation + Taxa + (1 | Site)</td><td>8</td><td>1164.86</td><td>97.82</td></tr>
<tr><td>Abundance ~ Treatment + Time + Temperature + Elevation + Taxa + (1 | Site) + Temperature:Elevation</td><td>9</td><td>1165.23</td><td>98.19</td></tr>
<tr><td>Abundance ~ Taxa + Treatment + Time + Temperature + Taxa:Time + Taxa:Temperature + (1 | Site)</td><td>9</td><td>1166.46</td><td>99.43</td></tr>
<tr><td>Abundance ~ Treatment + Time + Taxa + (1 | Site)</td><td>6</td><td>1169.00</td><td>101.97</td></tr>
<tr><td>Abundance ~ Taxa + Treatment + Time + Taxa:Time + (1 | Site)</td><td>7</td><td>1169.36</td><td>102.32</td></tr>
<tr><td>Abundance ~ Treatment + Time + Elevation + Taxa + (1 | Site)</td><td>7</td><td>1171.11</td><td>104.08</td></tr>
<tr><td>Abundance ~ Treatment + Taxa + (1 | Site)</td><td>5</td><td>1171.83</td><td>104.80</td></tr>
<tr><td>Abundance ~ Treatment + Elevation + Taxa + (1 | Site)</td><td>6</td><td>1173.77</td><td>106.73</td></tr>
</table>

Appendix 21: GLMM results of *Creophilus erythrocephalus* (predator) and *Ptomophila lacrymosa* (scavenger) abundance in response to experimental exclusion of vertebrates and abiotic factors. Note a positive response in taxa favors *P. lacrymosa*.

	β	2.5 %	97.5 %	se	z	p	sig.
(Intercept)	2.754	2.4	3.1	0.162	17.044	3.8E-65	
Taxa	1.099	0.7	1.5	0.181	6.090	1.1E-09	***
Treatment	-0.192	-0.5	0.2	0.179	-1.070	0.285	
Time	0.750	0.2	1.3	0.274	2.733	0.006	**
Temperature	0.293	-0.3	0.9	0.286	1.023	0.306	
Time × Temperature	-1.351	-1.6	-1.1	0.120	-11.242	2.5E-29	***
Taxa × Time	-0.737	-1.4	0.0	0.351	-2.100	0.036	*
Taxa × Temperature	0.360	-0.4	1.1	0.370	0.972	0.331	

Appendix 22: GLMM model of fly abundance's response to experimental exclusion of vertebrates and associated abiotic variables.

Variable	β	2.5 %	97.5 %	se	z	p	sig.
(Intercept)	4.184	3.8	4.6	0.219	19.130	1.4E-81	
Treatment	0.054	-0.5	0.6	0.260	0.206	0.837	
Time	0.201	-0.3	0.7	0.259	0.777	0.437	
Temperature	0.137	-0.4	0.7	0.292	0.468	0.640	
Time × Temperature	-0.866	-1.1	-0.6	0.142	-6.105	1.0E-09	***

Appendix 23: A model selection table for blow flies and flesh flies in response to experimental restriction of vertebrates and permutations of abiotic variables.

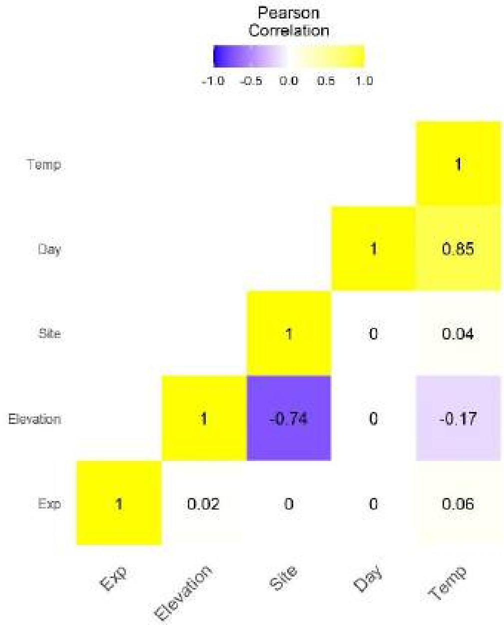
<table>
<tr><th>Model</th><th>K</th><th>AICc</th><th>ΔAICc</th></tr>
<tr><td>Abundance ~ Taxa + Treatment + Time + Temperature + Time:Temperature + Taxa:Time + Taxa:Temperature + (1 | Site)</td><td>10</td><td>803.56</td><td>0.00</td></tr>
<tr><td>Abundance ~ Taxa + Treatment + Time + Elevation + Time:Temperature + Temperature:Elevation + Taxa:Time + (1 | Site)</td><td>10</td><td>806.31</td><td>2.76</td></tr>
<tr><td>Abundance ~ Taxa + Treatment + Time + Temperature + Elevation + Time:Temperature + Temperature:Elevation + Taxa:Time + Taxa:Temperature + (1 | Site)</td><td>12</td><td>807.33</td><td>3.77</td></tr>
<tr><td>Abundance ~ Treatment + Time + Temperature + Taxa + (1 | Site) + Time:Temperature</td><td>8</td><td>809.75</td><td>6.19</td></tr>
<tr><td>Abundance ~ Treatment + Time + Temperature + Elevation + Taxa + (1 | Site) + Time:Temperature</td><td>9</td><td>811.02</td><td>7.46</td></tr>
<tr><td>Abundance ~ Taxa + Treatment + Temperature + Elevation + Time:Temperature + Temperature:Elevation + Taxa:Temperature + (1 | Site)</td><td>10</td><td>811.68</td><td>8.13</td></tr>
<tr><td>Abundance ~ Treatment + Time + Temperature + Elevation + Taxa + (1 | Site) + Time:Temperature + Temperature:Elevation</td><td>10</td><td>813.30</td><td>9.74</td></tr>
<tr><td>Abundance ~ Taxa + Treatment + Time + Temperature + Taxa:Time + Taxa:Temperature + (1 | Site)</td><td>9</td><td>831.75</td><td>28.19</td></tr>
<tr><td>Abundance ~ Taxa + Treatment + Time + Taxa:Time + (1 | Site)</td><td>7</td><td>833.40</td><td>29.84</td></tr>
<tr><td>Abundance ~ Treatment + Temperature + Elevation + Taxa + (1 | Site)</td><td>7</td><td>835.16</td><td>31.61</td></tr>
<tr><td>Abundance ~ Treatment + Temperature + Taxa + (1 | Site)</td><td>6</td><td>836.29</td><td>32.73</td></tr>
</table>

Abundance ~ Treatment + Time + Temperature + Elevation + Taxa + (1 | Site)	8	836.57	33.01
Abundance ~ Treatment + Temperature + Elevation + Taxa + (1 | Site) + Temperature:Elevation	8	836.58	33.02
Abundance ~ Treatment + Time + Temperature + Elevation + Taxa + (1 | Site) + Temperature:Elevation	9	838.03	34.47
Abundance ~ Taxa + Treatment + Temperature + Taxa:Temperature + (1 | Site)	7	838.26	34.70
Abundance ~ Treatment + Time + Temperature + Taxa + (1 | Site)	7	838.31	34.75
Abundance ~ Treatment + Time + Taxa + (1 | Site)	6	840.83	37.27
Abundance ~ Treatment + Time + Elevation + Taxa + (1 | Site)	7	841.51	37.96
Abundance ~ Treatment + Elevation + Taxa + (1 | Site)	6	842.54	38.98
Abundance ~ Treatment + Taxa + (1 | Site)	5	842.63	39.07

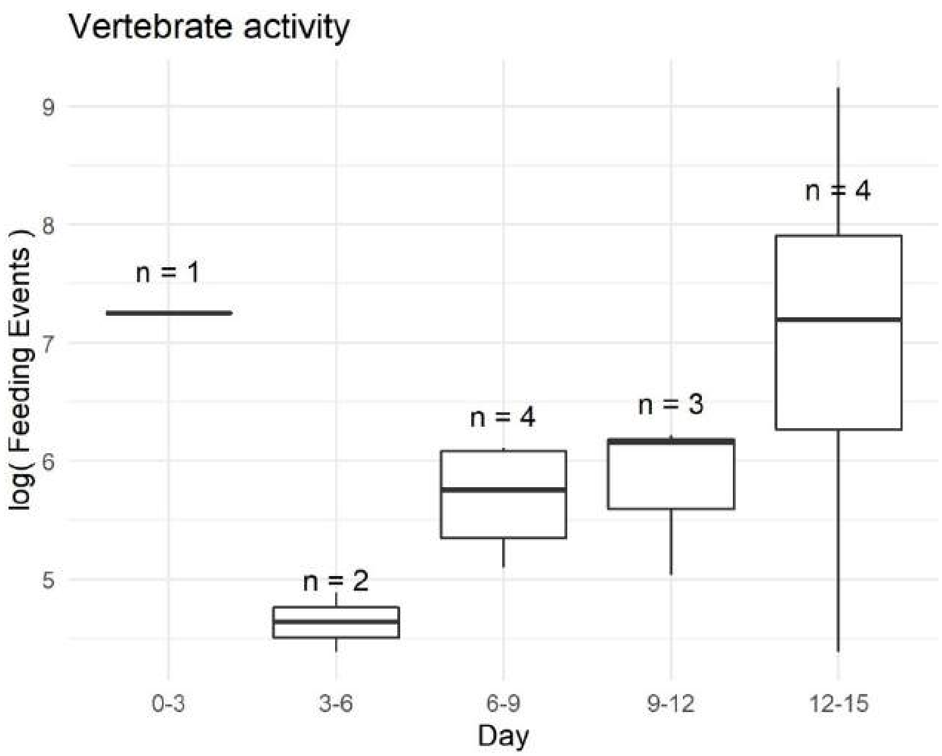
Appendix 24: Model results from GLMM of blow fly and flesh fly abundance in response to experimental exclusion of vertebrate scavengers and abiotic factors.

	β	2.5 %	97.5 %	se	z	p	sig.
(Intercept)	0.927	0.5	1.3	0.199	4.656	3.2E-06	
Taxa	1.359	1.0	1.7	0.195	6.976	3.0E-12	***
Treatment	0.392	0.0	0.8	0.192	2.040	0.041	*
Time	0.682	0.2	1.2	0.256	2.660	0.008	**
Temperature	-0.177	-0.7	0.4	0.292	-0.608	0.543	
Time × Temperature	-0.695	-0.9	-0.5	0.115	-6.057	1.4E-09	***
Taxa × Time	-0.986	-1.6	-0.3	0.326	-3.026	0.002	**
Taxa × Temperature	0.544	-0.2	1.3	0.364	1.495	0.135	

Appendix 25: Pearson correlation of variables. Note temperature and day have a high positive correlation due to weather patterns that warmed over the study period. Site and elevation are negatively correlated due to picking sites that don't share elevation.



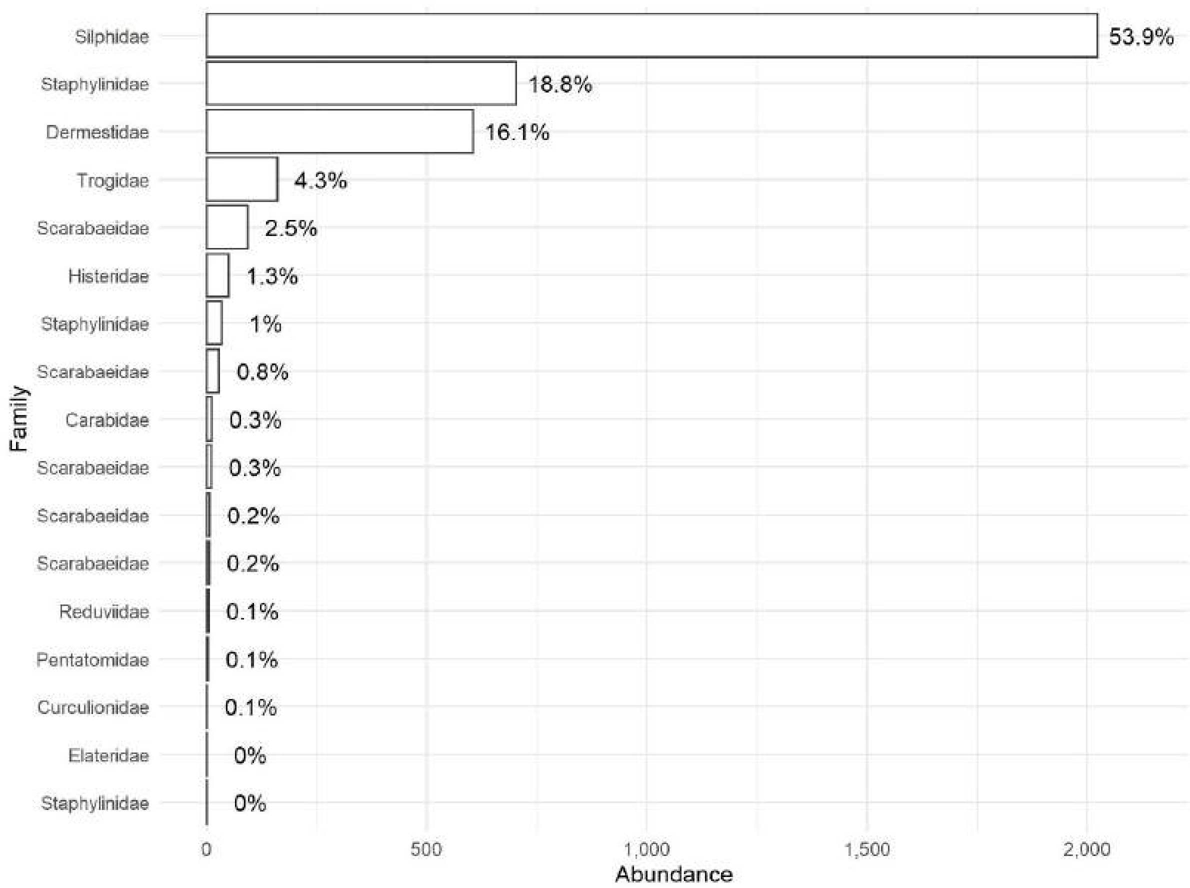
Appendix 26: Mean count of vertebrate feeding activity (log-scaled) at exposed sites during the first fifteen days of decomposition. Number of carcasses visited in a single sampling period (72hr) indicated above each upper quantile. No more than four carcasses were fed upon by vertebrates during a single sampling period. As time increases so does the number of vertebrates visiting due to vertebrate discovery of carcasses.



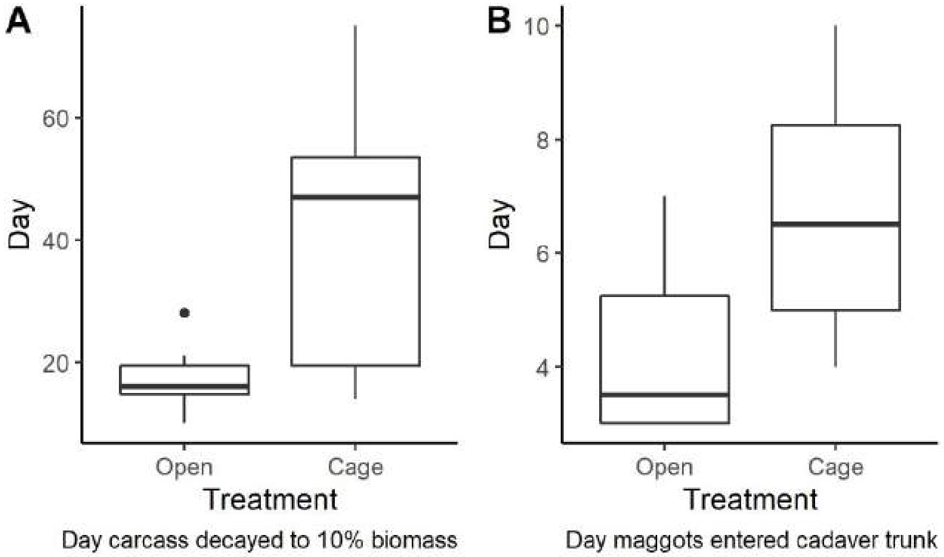
Appendix 27: Vertebrate feeding behaviour at carcasses during the first fifteen days of carrion decomposition with 72-hour sampling periods. Out of a total of 8 carcasses, the maximum number of carcasses visited during a single sampling period was 4.

Sample Period	Number of carcasses visited	Feeding Events			
		Sum	μ	σ	Percent Total
0-3	1	1,408	176.0	497.8	8.6%
3-6	2	212	26.5	51.0	1.3%
6-9	4	1,278	159.8	195.4	7.8%
9-12	3	1,127	140.9	220.0	6.9%
12-15	4	12,350	1,543.8	3,278.4	75.4%

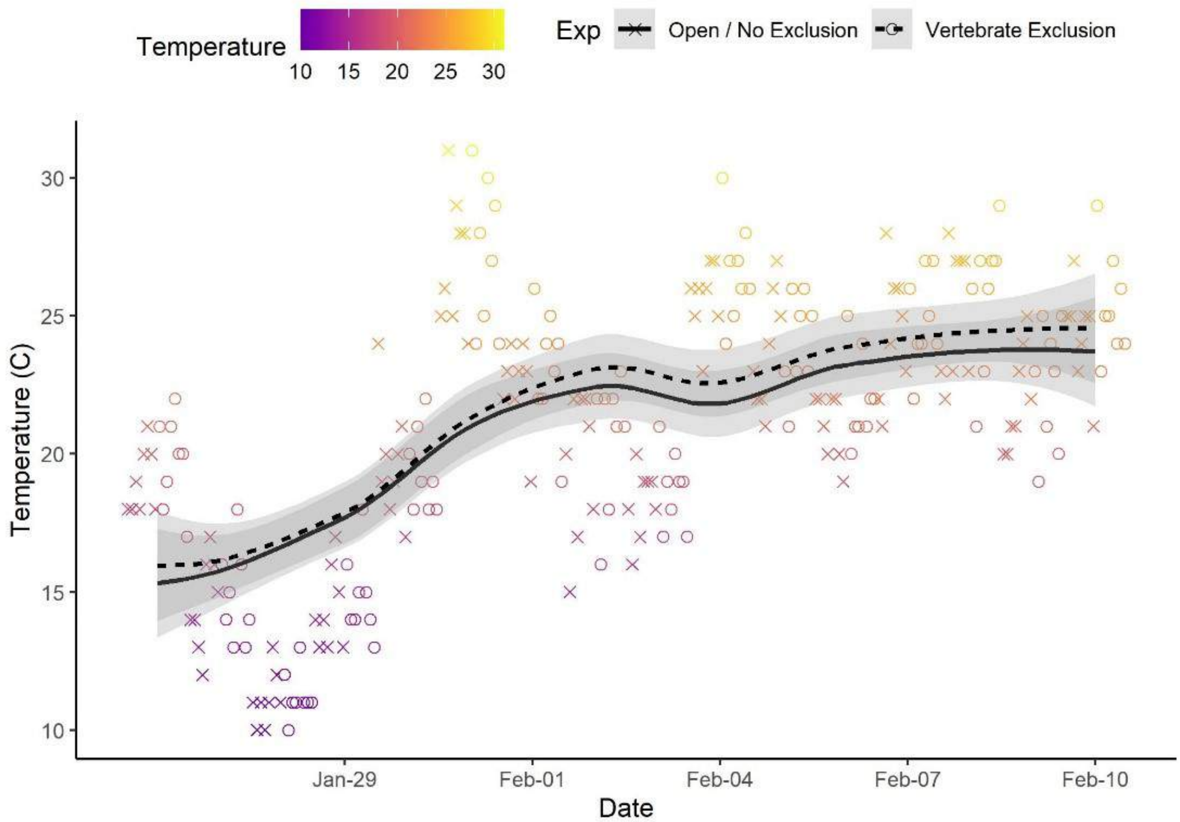
Appendix 28: Assemblage of beetle morpho-species family names of beetles appearing in pitfall traps. The most abundant is *Ptomophila lacrymosa* followed by *Creophilus erythrocephalus*.



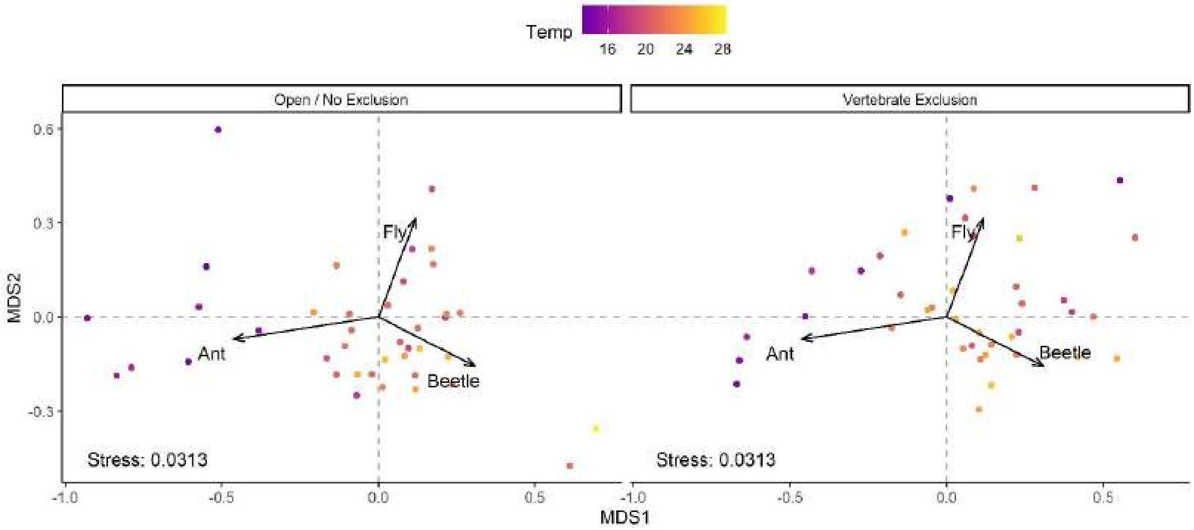
Appendix 29: Decay events during summer decomposition between open and vertebrate exclusion treatments. A) Mean day at which carcasses decayed to 10% biomass. B) Mean day at which maggot mass was observed in trunk (body cavity) of kangaroo cadaver.



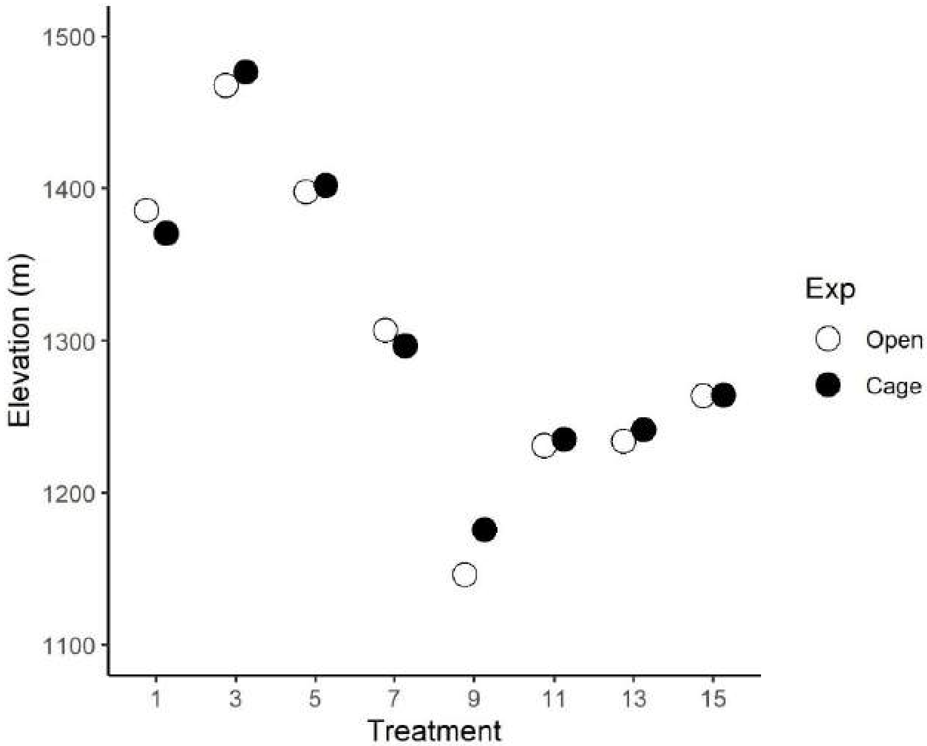
Appendix 30: Daily temperatures recorded at 14:00 at all carcasses during the summer replicate. Date labels correspond to insect collection dates.



Appendix 31: MDS visualisation of insect taxa (ants, beetles, and flies) in relation to site temperatures during the summer replicate.

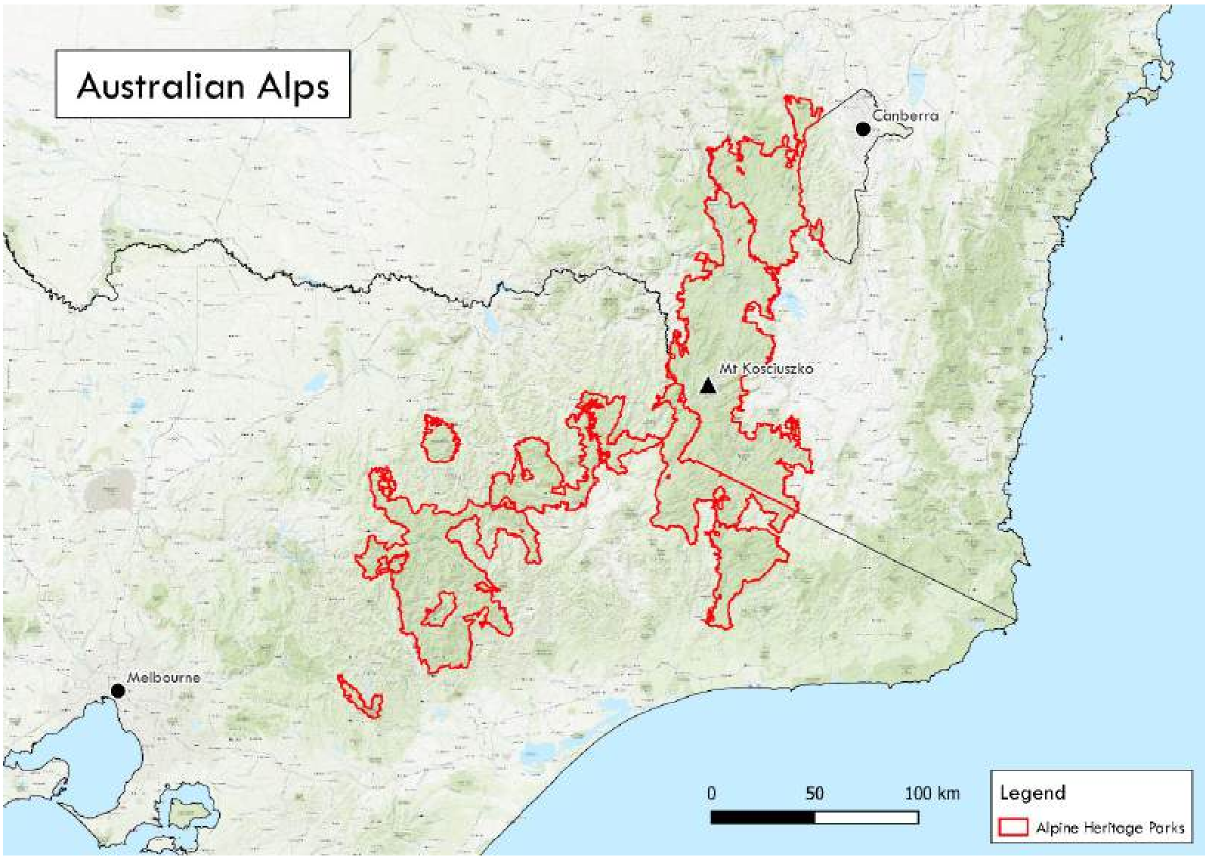


Appendix 32: Altitude in meters above sea level of each summer treatment site.

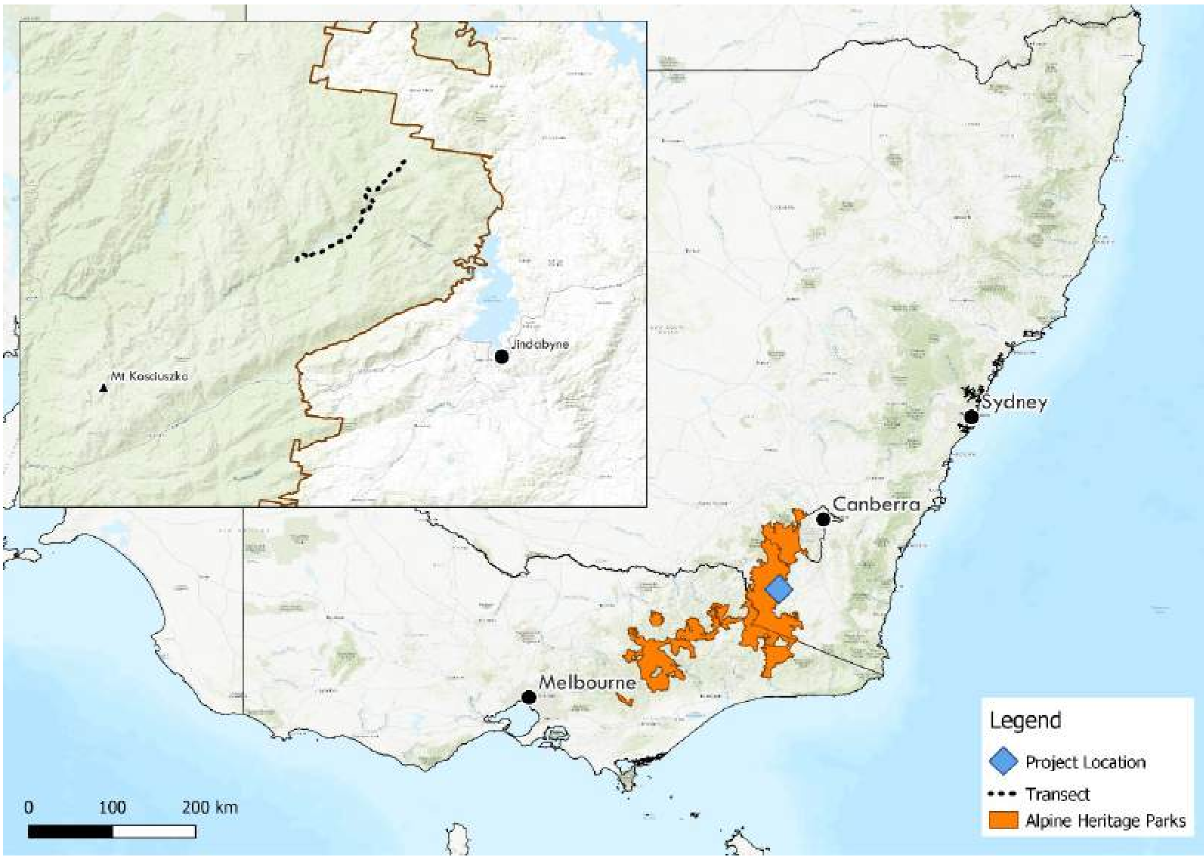


Maps

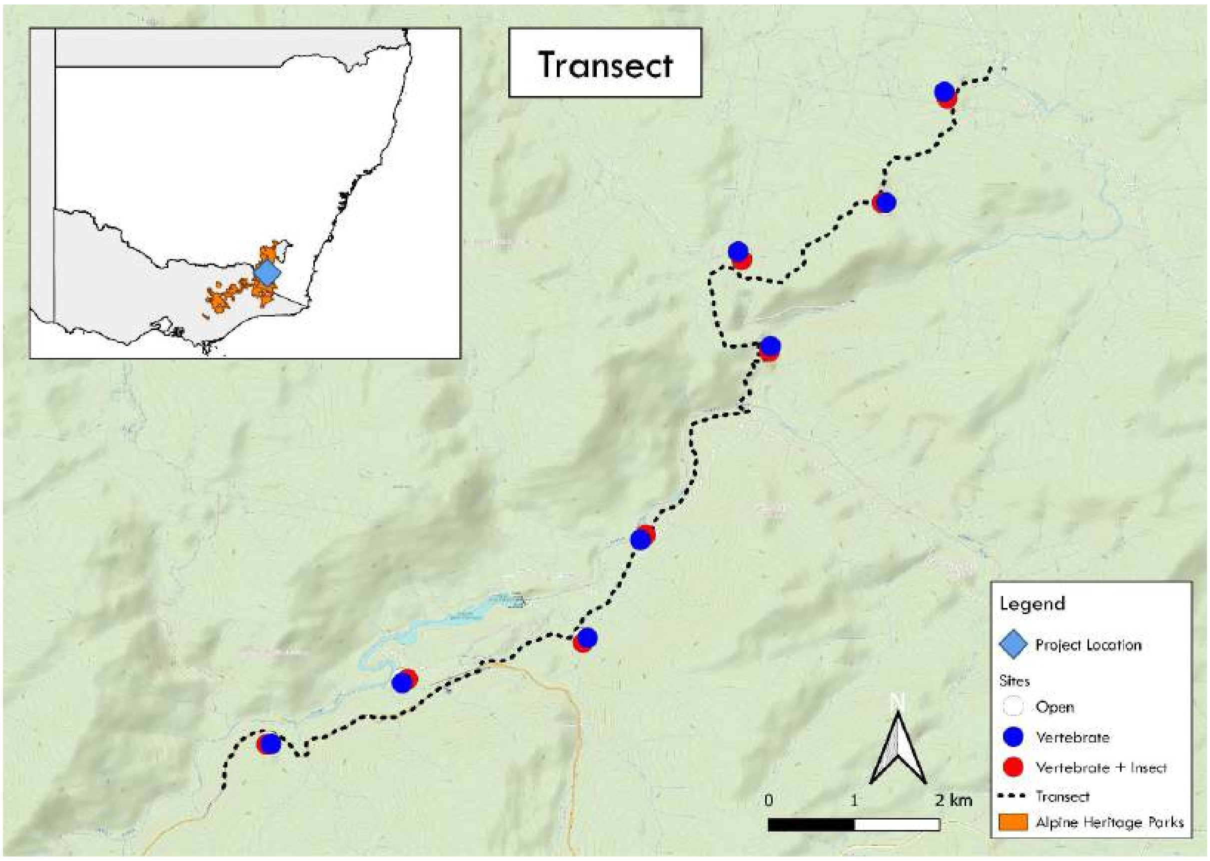
Appendix 33: A map of the National Alpine Heritage Parks of Australia. This contains much of the Australian Alps (Snowy Mountains) of which Mt Kosciuszko sits in the middle of.



Appendix 34: A map showing the continental location of the Australian Alps as well as an overview map of the study transect in Kosciuszko NP.



Appendix 35: A map showing the study transect and its location in Kosciuszko NP.



References: Master List

Allen, M., Elbroch, L., Casady, D., Wittmer, H., 2014. Seasonal variation in the feeding ecology of pumas (Puma concolor) in northern California. Canadian Journal of Zoology 92, 397–403. https://doi.org/10.1139/cjz-2013-0284

Anderson, G.S., Barton, P.S., Archer, M., Wallace, J.R., 2019. Invertebrate Scavenging Communities, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 45–69. https://doi.org/10.1007/978-3-030-16501-7_3

Anderson, G.S., VanLaerhoven, S.L., 1996. Initial Studies on Insect Succession on Carrion in Southwestern British Columbia. J. Forensic Sci. 41, 13964J. https://doi.org/10.1520/JFS13964J

Archer, M.S., 2004. Rainfall and temperature effects on the decomposition rate of exposed neonatal remains. Sci Justice 44, 35–41. https://doi.org/10.1016/S1355-0306(04)71683-4

Archer, M.S., 2003. Annual variation in arrival and departure times of carrion insects at carcasses: implications for succession studies in forensic entomology. Aust. J. Zool. 51, 569. https://doi.org/10.1071/ZO03053

Australian Bureau of Statistics, 2012. The Snowy Mountains Hydro-Electric Scheme [WWW Document]. Australian Bureau of Statistics. URL https://www.abs.gov.au/ausstats/abs@.nsf/0/FDE81AE268C76207CA2569DE00274C14?Open# (accessed 8.15.21).

Bajerlein, D., Matuszewski, S., Konwerski, S., 2011. Insect succession on carrion: Seasonality, habitat preference and residency of histerid beetles (Coleoptera: Histeridae) visiting pig carrion exposed in various forests (Western Poland). Polish Journal of Ecology 59, 789–797.

Barton, P.S., Bump, J.K., 2019. Carrion Decomposition, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 101–124. https://doi.org/10.1007/978-3-030-16501-7_5

Barton, P.S., Cunningham, S.A., Lindenmayer, D.B., Manning, A.D., 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia 171, 761–772. https://doi.org/10.1007/s00442-012-2460-3

Barton, P.S., Evans, M.J., 2017. Insect biodiversity meets ecosystem function: differential effects of habitat and insects on carrion decomposition. Ecological Entomology 42, 364–374. https://doi.org/10.1111/een.12395

Barton, P.S., Evans, M.J., Foster, C.N., Pechal, J.L., Bump, J.K., Quaggiotto, M.-M., Benbow, M.E., 2019. Towards Quantifying Carrion Biomass in Ecosystems. Trends in Ecology & Evolution 34, 950–961. https://doi.org/10.1016/j.tree.2019.06.001

Barton, P.S., Evans, M.J., Pechal, J.L., Benbow, M.E., 2017. Necrophilous Insect Dynamics at Small Vertebrate Carrion in a Temperate Eucalypt Woodland. Journal of Medical Entomology 54, 964–973. https://doi.org/10.1093/jme/tjw242

Bastolla, U., Fortuna, M.A., Pascual-García, A., Ferrera, A., Luque, B., Bascompte, J., 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature 458, 1018–1020. https://doi.org/10.1038/nature07950

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Baz, A., Cifrián, B., Díaz-äranda, L.M., Martín-Vega, D., 2007. The distribution of adult blow-flies (Diptera: Calliphoridae) along an altitudinal gradient in Central Spain. Annales de la Société entomologique de France (N.S.) 43, 289–296. https://doi.org/10.1080/00379271.2007.10697524

Beasley, J.C., Olson, Z.H., DeVault, T.L., 2015. Ecological role of vertebrate scavengers. CRC Press. https://doi.org/10.1201/b18819

Beasley, J.C., Olson, Z.H., Devault, T.L., 2012. Carrion cycling in food webs: Comparisons among terrestrial and marine ecosystems. Oikos 121, 1021–1026. https://doi.org/10.1111/j.1600-0706.2012.20353.x

Beasley, J.C., Olson, Z.H., Selva, N., DeVault, T.L., 2019. Ecological Functions of Vertebrate Scavenging, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 125–157. https://doi.org/10.1007/978-3-030-16501-7_6

Benbow, M., Barton, P., Ulyshen, M., Beasley, J., DeVault, T., Strickland, M., Tomberlin, J., Jordan, H., Pechal, J., 2019. Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. Ecological Monographs 89. https://doi.org/10.1002/ecm.1331

Benbow, M., Lewis, A., Tomberlin, J., Pechal, J., 2013. Seasonal Necrophagous Insect Community Assembly During Vertebrate Carrion Decomposition. Journal of Medical Entomology 50, 440–450. https://doi.org/10.1603/ME12194

Benbow, M.E., Pechal, J.L., Mohr, R.M., 2015a. Community and Landscape Ecology of Carrion, in: Carrion Ecology, Evolution, and Their Applications. CRC Press.

Benbow, M.E., Tomberlin, J.K., Tarone, A.M. (Eds.), 2015b. Carrion Ecology, Evolution, and Their Applications. CRC Press, Boca Raton. https://doi.org/10.1201/b18819

Biggs, C.R., Yeager, L.A., Bolser, D.G., Bonsell, C., Dichiera, A.M., Hou, Z., Keyser, S.R., Khursigara, A.J., Lu, K., Muth, A.F., Negrete, B., Erisman, B.E., 2020. Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. Ecosphere 11, e03184. https://doi.org/10.1002/ecs2.3184

Bird, M.I., Hutley, L.B., Lawes, M.J., Lloyd, J., Luly, J.G., Ridd, P.V., Roberts, R.G., Ulm, S., Wurster, C.M., 2013. Humans, megafauna and environmental change in tropical Australia. Journal of Quaternary Science 28, 439–452. https://doi.org/10.1002/jqs.2639

Bourel, B., Martin-Bouyer, L., Hedouin, V., Cailliez, J., Derout, D., Gosset, D., 1999. Necrophilous insect succession on rabbit carrion in sand dune habitats in northern France. Journal of Medical Entomology 36, 420–425. https://doi.org/10.1093/jmedent/36.4.420

Braack, L.E.O., 1987. Community dynamics of carrion-attendant arthropods in tropical african woodland. Oecologia 72, 402–409. https://doi.org/10.1007/BF00377571

Bradshaw, C.J.A., 2012. Little left to lose: deforestation and forest degradation in Australia since European colonization. Journal of Plant Ecology 5, 109–120. https://doi.org/10.1093/jpe/rtr038

Braithwaite, R.W., 1990. Australia's Unique Biota: Implications for Ecological Processes. Journal of Biogeography 17, 347–354. https://doi.org/10.2307/2845364

Brown, D., Thomas, E., Herbert, K., Primrose, K., 2016. Evaluating the effects of feral deer management on endangered alpine peatlands: The Alpine National Park deer control trial. Plant Protection Quarterly 31, 63.

Brown, O.J.F., 2006. Tasmanian devil (Sarcophilus harrisii) extinction on the Australian mainland in the mid-Holocene: multicausality and ENSO intensification. Alcheringa: An Australasian Journal of Palaeontology 30, 49–57. https://doi.org/10.1080/03115510609506855

Bureau of Meteorology, 2020. Summary statistics MOUNT KOSCIUSKO (HOTEL KOSCIUSKO) [WWW Document]. URL http://www.bom.gov.au/climate/averages/tables/cw_071012.shtml (accessed 11.3.20).

Burkepile, D., Parker, J., Woodson, C., Mills, H., Kubanek, J., Sobecky, P., Hay, M., 2006. Chemically mediated competition between microbes and animals: Microbes as consumers in food webs. Ecology 87, 2821–2831. https://doi.org/10.1890/0012-9658(2006)87[2821:CMCBMA]2.0.CO;2

Byrd, J.H., Tomberlin, J.K. (Eds.), 2019. Forensic Entomology: The Utility of Arthropods in Legal Investigations, 3rd ed. CRC Press, Boca Raton. https://doi.org/10.4324/9781351163767

Cairns, S., 2020. The results of a survey of the wild horse populations in the Kosciuszko National Park. G.E and S.C. Cairns Consulting Pty. Ltd. Armidale.

Cardinale, B., Srivastava, D., Duffy, J., Wright, J., Downing, A., Sankaran, M., Jouseau, C., 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443, 989–92. https://doi.org/10.1038/nature05202

Carter, D.O., Yellowlees, D., Tibbett, M., 2007. Cadaver decomposition in terrestrial ecosystems. Naturwissenschaften 94, 12–24. https://doi.org/10.1007/s00114-006-0159-1

Charabidze, D., Trumbo, S., Grzywacz, A., Costa, J.T., Benbow, M.E., Barton, P.S., Matuszewski, S., 2021. Convergence of Social Strategies in Carrion Breeding Insects. BioScience 71, 1028–1037. https://doi.org/10.1093/biosci/biab068

Cook, D.E., 2021. Anthropogenic environmental change on the frontiers of European colonisation in Australia, A.D. 1788–1840. A reply to comments in Woodward (2020). Geomorphology 373, 107234. https://doi.org/10.1016/j.geomorph.2020.107234

Cook, D.E., 2019. Butzer ‘Down Under’: Debates on anthropogenic erosion in early Colonial Australia. Geomorphology 331, 160–174. https://doi.org/10.1016/j.geomorph.2018.12.011

Cook, R., Jovanović, S., 2019. The Emu Strikes Back: An Inquiry into Australia’s Peculiar Military Action of 1932. Romanian Journal of Historical Studies 2, 1–11.

Costin, A.B., 2000. Kosciuszko alpine flora, 2nd ed. ed. CSIRO Publishing, Melbourne.

Crippen, T.L., Benbow, M.E., Pechal, J.L., 2015. Microbial Interactions during Carrion Decomposition, in: Carrion Ecology, Evolution, and Their Applications. CRC Press.

CSIRO, 2012. What Bug Is That? The guide to Australian insect families. [WWW Document]. Taxonomy Research & Information Network. URL http://anic.ento.csiro.au/insectfamilies/ (accessed 10.17.21).

Cunningham, C.X., Johnson, C.N., Barmuta, L.A., Hollings, T., Woehler, E.J., Jones, M.E., 2018. Top carnivore decline has cascading effects on scavengers and carrion persistence. Proceedings. Biological sciences 285. https://doi.org/10.1098/rspb.2018.1582

De Jong, G.D., Chadwick, J.W., 1999. Decomposition and Arthropod Succession on Exposed Rabbit Carrion During Summer at High Altitudes in Colorado, USA. J Med Entomol 36, 833–845. https://doi.org/10.1093/jmedent/36.6.833

Delignette-Muller, M.L., Dutang, C., 2015. fitdistrplus: An R Package for Fitting Distributions. Journal of Statistical Software 64, 1–34. https://doi.org/10.18637/jss.v064.i04

DeVault, T.L., Brisbin, Jr., I.L., Rhodes, Jr., O.E., 2004. Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers. Can. J. Zool. 82, 502–509. https://doi.org/10.1139/z04-022

DeVault, T.L., Jr, O.E.R., Shivik, J.A., 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102, 225–234. https://doi.org/10.1034/j.1600-0706.2003.12378.x

DeVault, T.L., Rhodes, O.E., 2002. Identification of vertebrate scavengers of small mammal carcasses in a forested landscape. Acta Theriol 47, 185–192. https://doi.org/10.1007/BF03192458

Devault, T.L., Rhodes, O.E., Shivik, J.A., Devault, T.L., Rhodes, O.E., Shivik, J.A., 2003. Scavenging by Vertebrates : Behavioral , Ecological , and Evolutionary Perspectives on an Important Energy Transfer Pathway in Terrestrial Ecosystems Published by : Wiley on behalf of Nordic Society Oikos Stable URL : http://www.jstor. Oikos 102, 225–234.

Dickman, C.R., 1996. Impact of exotic generalist predators on the native fauna of Australia. wbio 2, 185–195. https://doi.org/10.2981/wlb.1996.018

Driscoll, D.A., Worboys, G.L., Allan, H., Banks, S.C., Beeton, N.J., Cherubin, R.C., Doherty, T.S., Finlayson, C.M., Green, K., Hartley, R., Hope, G., Johnson, C.N., Lintermans, M., Mackey, B., Paull, D.J., Pittock, J., Porfirio, L.L., Ritchie, E.G., Sato, C.F., Scheele, B.C., Slattery, D.A., Venn, S., Watson, D., Watson, M., Williams, R.M., 2019. Impacts of feral horses in the Australian Alps and evidence-based solutions. Ecological Management and Restoration 20, 63–72. https://doi.org/10.1111/emr.12357

Environment, Energy and Science, 2019. 2020 Quota Report New South Wales Commercial Kangaroo Harvest Management Plan 2017-21. Department of Planning, Industry and Environment.

Evans, M., Wallman, J., Barton, P., 2020. Traits reveal ecological strategies driving carrion insect community assembly. Ecological Entomology 45, 966–977. https://doi.org/10.1111/een.12869

Farwig, N., Brandl, R., Siemann, S., Wiener, F., Müller, J., 2014. Decomposition rate of carrion is dependent on composition not abundance of the assemblages of insect scavengers. Oecologia 175, 1291–1300. https://doi.org/10.1007/s00442-014-2974-y

Fetzer, I., Johst, K., Schäwe, R., Banitz, T., Harms, H., Chatzinotas, A., 2015. The extent of functional redundancy changes as species' roles shift in different environments. PNAS 112, 14888–14893. https://doi.org/10.1073/pnas.1505587112

Fillios, M., Gordon, C., Koch, F., Letnic, M., 2010. The effect of a top predator on kangaroo abundance in arid Australia and its implications for archaeological faunal assemblages. Journal of Archaeological Science 37, 986–993. https://doi.org/10.1016/j.jas.2009.11.031

Fonseca, C.R., Ganade, G., 2001. Species functional redundancy, random extinctions and the stability of ecosystems. Journal of Ecology 89, 118–125. https://doi.org/10.1046/j.1365-2745.2001.00528.x

Forsyth, D., Latham, A., Davis, N., Caley, P., Letnic, M., Moloney, P., Woodford, L., Woolnough, A., 2019. Interactions between dingoes and introduced wild ungulates: concepts, evidence and knowledge gaps. Australian Mammalogy 41, 12–26. https://doi.org/10.1071/AM17042

George, K.A., Archer, M.S., Toop, T., 2013. Abiotic environmental factors influencing blowfly colonisation patterns in the field. Forensic Science International 229, 100–107. https://doi.org/10.1016/j.forsciint.2013.03.033

Gill, A.M., 1975. Fire and The Australian Flora: A Review. Australian Forestry 38, 4–25. https://doi.org/10.1080/00049158.1975.10675618

Gomo, G., Rød-Eriksen, L., Andreassen, H.P., Mattisson, J., Odden, M., Devineau, O., Eide, N.E., 2020. Scavenger community structure along an environmental gradient from boreal forest to alpine tundra in Scandinavia. Ecology and Evolution 10, 12860–12869. https://doi.org/10.1002/ece3.6834

Green, K., Pickering, C.M., 2002. A Scenario for Mammal and Bird Diversity in the Snowy Mountains of Australia in Relation to Climate Change, in: Mountain Biodiversity. Routledge.

Hall, G.P., Gill, K.P., 2005. Management of Wild Deer in Australia. The Journal of Wildlife Management 69, 837–844. https://doi.org/10.2193/0022-541X(2005)069[0837:MOWDIA]2.0.CO;2

Hill, J.E., DeVault, T.L., Beasley, J.C., Rhodes, O.E., Belant, J.L., 2018. Effects of vulture exclusion on carrion consumption by facultative scavengers. Ecology and Evolution 8, 2518–2526. https://doi.org/10.1002/ece3.3840

Holm, S., 1979. A Simple Sequentially Rejective Multiple Test Procedure. Scandinavian Journal of Statistics 6, 65–70.

Hope, G., Mooney, S.D., Allen, K., Baker, P., Keaney, B., Kemp, J., Martin, L., Pearson, S., Stevenson, J., Zheng, X., 2019. Science through time: Understanding the archive at rennix gap bog, a sub-alpine peatland in kosciuszko national park, New South Wales, Australia. Proceedings of the Linnean Society of New South Wales 141, 25–47.

Houston, D.C., 1985. Evolutionary Ecology of Afrotropical and Neotropical Vultures in Forests. Ornithological Monographs 856–864. https://doi.org/10.2307/40168321

Hrdina, F., 2014. Marsupial destruction in Queensland 1877-1930. Australian Zoologist 30, 272–286. https://doi.org/10.7882/AZ.1997.003

Huijbers, C.M., Schlacher, T.A., Schoeman, D.S., Olds, A.D., Weston, M.A., Connolly, R.M., 2015. Limited functional redundancy in vertebrate scavenger guilds fails to compensate for the loss of raptors from urbanized sandy beaches. Diversity and Distributions 21, 55–63. https://doi.org/10.1111/ddi.12282

Independent Scientific Committee (N.S.W.), 2003. An assessment of the values of Kosciuszko National Park : interim report. National Parks and Wildlife Service, Queanbeyan NSW.

Kalinova, B., Podskalska, H., Ruzicka, J., Hoskovec, M., 2009. Irresistible bouquet of death-how are burying beetles (Coleoptera: Silphidae: Nicrophorus) attracted by carcasses. Naturwissenschaften 96, 889–899. https://doi.org/10.1007/s00114-009-0545-6

Kassambara, A., Kosinski, M., Biecek, P., 2021. survminer: Drawing Survival Curves using “ggplot2.”

KR Norris, 1966. Daily patterns of flight activity of blowflies (Calliphoridae : Diptera) in the Canberra district as indicated by trap catches. Australian journal of zoology 14, 865–853. https://doi.org/10.1071/ZO9660835

Latham, A.D.M., Cecilia Latham, M., Herries, D., Barron, M., Cruz, J., Anderson, D.P., 2018. Assessing the efficacy of aerial culling of introduced wild deer in New Zealand with analytical decomposition of predation risk. Biol Invasions 20, 251–266. https://doi.org/10.1007/s10530-017-1531-0

Lauber, C.L., Metcalf, J.L., Keepers, K., Ackermann, G., Carter, D.O., Knight, R., 2014. Vertebrate Decomposition Is Accelerated by Soil Microbes. Appl. Environ. Microbiol. 80, 4920–4929. https://doi.org/10.1128/AEM.00957-14

Lawrence, S., Davies, P., 2011. An Archaeology of Australia Since 1788, Contributions To Global Historical Archaeology. Springer New York, New York, NY. https://doi.org/10.1007/978-1-4419-7485-3

Lawton, J.H., Brown, V.K., 1994. Redundancy in Ecosystems, in: Schulze, E.-D., Mooney, H.A. (Eds.), Biodiversity and Ecosystem Function, Praktische Zahnmedizin Odonto-Stomatologie Pratique Practical Dental Medicine. Springer, Berlin, Heidelberg, pp. 255–270. https://doi.org/10.1007/978-3-642-58001-7_12

Mace, G.M., Norris, K., Fitter, A.H., 2012. Biodiversity and ecosystem services: a multilayered relationship. Trends in Ecology & Evolution 27, 19–26. https://doi.org/10.1016/j.tree.2011.08.006

Mansergh, I., Newsome, A., Shorthouse, D., 2003. Fauna Values, in: An Assessment of the Values of Kosciuszko National Park. NSW National Parks and Wildlife Service, Queanbeyan NSW.

Markandya, A., Taylor, T., Longo, A., Murty, M.N., Murty, S., Dhavala, K., 2008. Counting the cost of vulture decline—An appraisal of the human health and other benefits of vultures in India. Ecological Economics, Special Section: Biodiversity and Policy 67, 194–204. https://doi.org/10.1016/j.ecolecon.2008.04.020

Mateo-Tomás, P., Olea, P.P., Moleón, M., Vicente, J., Botella, F., Selva, N., Viñuela, J., Sánchez-Zapata, J.A., 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. Diversity and Distributions 21, 913–924. https://doi.org/10.1111/ddi.12330

Mellanby, K., 1939. Low Temperature and Insect Activity. Proceedings of the Royal Society of London. Series B, Biological Sciences 127, 473–487.

Merritt, R.W., Jong, G.D.D., 2015. Arthropod Communities in Terrestrial Environments, in: Carrion Ecology, Evolution, and Their Applications. CRC Press.

Moleón, M., Sánchez-Zapata, J.A., Sebastián-González, E., Owen-Smith, N., 2015. Carcass size shapes the structure and functioning of an African scavenging assemblage. Oikos 124, 1391–1403. https://doi.org/10.1111/oik.02222

Moleón, M., Sánchez-Zapata, J.A., Selva, N., Donázar, J.A., Owen-Smith, N., 2014. Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. Biological Reviews 89, 1042–1054. https://doi.org/10.1111/brv.12097

Moleón, M., Selva, N., Quaggiotto, M.M., Bailey, D.M., Cortés-Avizanda, A., DeVault, T.L., 2019. Carrion Availability in Space and Time, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 23–44. https://doi.org/10.1007/978-3-030-16501-7_2

Moriarty, A., 2004. The liberation, distribution, abundance and management of wild deer in Australia. Wildl. Res. 31, 291. https://doi.org/10.1071/WR02100

Mules, T., 2005. Economic Impacts of National Park Tourism on Gateway Communities: The Case of Kosciuszko National Park. Tourism Economics 11, 247–259. https://doi.org/10.5367/0000000054183513

Müller, D., Seton, M., Zahirovic, S., Williams, S., Matthews, K., Wright, N., Shephard, G., Maloney, K., Barnett-Moore, N., Hosseinpour, M., Bower, D., Cannon, J., 2016. Ocean Basin Evolution and Global-Scale Plate Reorganization Events Since Pangea Breakup. Annual Review of Earth and Planetary Sciences 44, 107–138. https://doi.org/10.1146/annurev-earth-060115-012211

Muñoz-Lozano, C., Martín-Vega, D., Martínez-Carrasco, C., Sánchez-Zapata, J.A., Morales-Reyes, Z., Gonzálvez, M., Moleón, M., 2019. Avoidance of carnivore carcasses by vertebrate scavengers enables colonization by a diverse community of carrion insects. PLOS ONE 14, e0221890. https://doi.org/10.1371/journal.pone.0221890

Munoz-Lozano, C., Martin-Vega, D., Martinez-Carrasco, C., Sanchez-Zapata, J.A., Morales-Reyes, Z., Gonzalvez, M., Moleon, M., 2019. Avoidance of carnivore carcasses by vertebrate scavengers enables colonization by a diverse community of carrion insects. PLoS One 14, e0221890. https://doi.org/10.1371/journal.pone.0221890

Murray-Darling Basin Authority, 2015. Murrumbidgee [WWW Document]. Murray–Darling Basin Authority. URL https://www.mdba.gov.au/water-management/catchments/murrumbidgee (accessed 8.15.21).

Naeem, S., 1998. Species Redundancy and Ecosystem Reliability. Conservation Biology 12, 39–45.

Neven, L.G., 2000. Physiological responses of insects to heat. Postharvest Biology and Technology 21, 103–111. https://doi.org/10.1016/S0925-5214(00)00169-1

New South Wales, Department of Environment and Conservation, Parks and Wildlife Division, New South Wales, Department of Environment and Conservation, 2006. Kosciuszko National Park plan of management: 2006. Dept. of Environment and Conservation NSW, Sydney South, N.S.W.

New South Wales National Parks and Wildlife Service, New South Wales, Department of Planning, I. and E., 2021. Kosciuszko National Park wild horse heritage management plan.

New South Wales National Parks and Wildlife Service, New South Wales, Office of Environment and Heritage, 2016. Draft wild horse management plan: Kosciuszko National Park.

New South Wales, Office of Environment and Heritage, New South Wales National Parks and Wildlife Service, 2012. Peat-forming bogs and fens of the Snowy Mountains of NSW: technical report. Office of Environment and Heritage, Sydney South.

Newsome, A., 1990. The control of vertebrate pests by vertebrate predators. Trends in Ecology & Evolution 5, 187–191. https://doi.org/10.1016/0169-5347(90)90208-U

Newsome, T.M., Barton, B., Buck, J.C., DeBruyn, J., Spencer, E., Ripple, W.J., Barton, P.S., 2021. Monitoring the dead as an ecosystem indicator. Ecology and Evolution 11, 5844–5856. https://doi.org/10.1002/ece3.7542

Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A.J., Dickman, C.R., 2015. The ecological effects of providing resource subsidies to predators. Global Ecology and Biogeography 24, 1–11. https://doi.org/10.1111/geb.12236

O'Brien, R.C., Forbes, S.L., Meyer, J., Dadour, I.R., 2007. A preliminary investigation into the scavenging activity on pig carcasses in Western Australia. Forensic Science, Medicine, and Pathology 3, 194–199. https://doi.org/10.1007/s12024-007-0016-3

O'Bryan, C.J., Braczkowski, A.R., Beyer, H.L., Carter, N.H., Watson, J.E.M., McDonald-Madden, E., 2018. The contribution of predators and scavengers to human well-being. Nat Ecol Evol 2, 229–236. https://doi.org/10.1038/s41559-017-0421-2

Ogada, D.L., Torchin, M.E., Kinnaird, M.F., Ezenwa, V.O., 2012. Effects of Vulture Declines on Facultative Scavengers and Potential Implications for Mammalian Disease Transmission: *Vulture Declines, Facultative Scavengers, and Disease Transmission*. Conservation Biology 26, 453–460. https://doi.org/10.1111/j.1523-1739.2012.01827.x

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M.D., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlinn, D., Ouellette, M.-H., Cunha, E.R., Smith, T., Stier, A., Braak, C.J.F.T., Weedon, J., 2022. vegan: Community Ecology Package.

Olea, P.P., Mateo-Tomas, P., 2009. The role of traditional farming practices in ecosystem conservation: The case of transhumance and vultures. BIOLOGICAL CONSERVATION 142, 1844–1853. https://doi.org/10.1016/j.biocon.2009.03.024

Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), 2019a. Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-030-16501-7

Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, José A., 2019b. Introduction to the Topic of Carrion Ecology and Management, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, José Antonio (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 1–20. https://doi.org/10.1007/978-3-030-16501-7_1

Olson, Z.H., Beasley, J.C., DeVault, T.L., Rhodes, O.E., 2012. Scavenger community response to the removal of a dominant scavenger. Oikos 121, 77–84. https://doi.org/10.1111/j.1600-0706.2011.19771.x

Orians, G.H., Milewski, A.V., 2007. Ecology of Australia: the effects of nutrient-poor soils and intense fires. Biological Reviews 82, 393–423. https://doi.org/10.1111/j.1469-185X.2007.00017.x

Parmenter, R.R., MacMahon, J.A., 2009. Carrion Decomposition and Nutrient Cycling in a Semiarid Shrub—Steppe Ecosystem. Ecological Monographs 79, 637–661.

Payne, J.A., 1965. A Summer Carrion Study of the Baby Pig Sus Scrofa Linnaeus. Ecology 46, 592–602. https://doi.org/10.2307/1934999

Pechal, J.L., Benbow, M.E., Crippen, T.L., Tarone, A.M., Tomberlin, J.K., 2014. Delayed insect access alters carrion decomposition and necrophagous insect community assembly. ECOSPHERE 5. https://doi.org/10.1890/ES14-00022.1

Peers, M.J.L., Konkolics, S.M., Lamb, C.T., Majchrzak, Y.N., Menzies, A.K., Studd, E.K., Boonstra, R., Kenney, A.J., Krebs, C.J., Martinig, A.R., McCulloch, B., Silva, J., Garland, L., Boutin, S., 2020. Prey availability and ambient temperature influence carrion persistence in the boreal forest. Journal of Animal Ecology n/a. https://doi.org/10.1111/1365-2656.13275

Pereira, L.M., Owen-Smith, N., Moleón, M., 2014. Facultative predation and scavenging by mammalian carnivores: Seasonal, regional and intra-guild comparisons. Mammal Review 44, 44–55. https://doi.org/10.1111/mam.12005

Prevention of Cruelty to Animals Amendment Act, 1997.

Putman, R.J., 1978. Flow of Energy and Organic Matter from a Carcase during Decomposition: Decomposition of Small Mammal Carrion in Temperate Systems. Oikos 31, 58–68. https://doi.org/10.2307/3543384

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ray, R.-R., H. Seibold, M. Heurich, 2014. Invertebrates outcompete vertebrate facultative scavengers in simulated lynx kills in the Bavarian Forest National Park, Germany. Animal biodiversity and conservation 37.

Read, J.L., Wilson, D., 2004. Scavengers and detritivores of kangaroo harvest offcuts in arid Australia. Wildl. Res. 31, 51. https://doi.org/10.1071/WR02051

Recinos-Aguilar, Y.M., García-García, M.D., Malo, E.A., Cruz-López, L., Rojas, J.C., 2019. The Colonization of Necrophagous Larvae Accelerates the Decomposition of Chicken Carcass and the Emission of Volatile Attractants for Blowflies (Diptera: Calliphoridae). Journal of Medical Entomology 56, 1590–1597. http://dx.doi.org.ezproxy.library.sydney.edu.au/10.1093/jme/tjz104

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and Ecological Effects of the World's Largest Carnivores. Science 343, 1241484–1241484. https://doi.org/10.1126/science.1241484

Rohr, R.P., Saavedra, S., Bascompte, J., 2014. On the structural stability of mutualistic systems. Science 345, 1253497–1253497. https://doi.org/10.1126/science.1253497

Rosenfeld, J.S., 2002. Functional redundancy in ecology and conservation. Oikos 98, 156–162. https://doi.org/10.1034/j.1600-0706.2002.980116.x

Sage, M.J.L., Towey, B.D., Brunner, J.L., 2019. Do scavengers prevent or promote disease transmission? The effect of invertebrate scavenging on Ranavirus transmission. Functional Ecology 33, 1342–1350. https://doi.org/10.1111/1365-2435.13335

Scherrer, P., Pickering, C.M., 2005. Recovery of Alpine Vegetation from Grazing and Drought: Data from Long-term Photoquadrats in Kosciuszko National Park, Australia. Arctic, Antarctic, and Alpine Research 37, 574–584. https://doi.org/10.1657/1523-0430(2005)037[0574:ROAVFG]2.0.CO;2

Sebastián-González, E., Barbosa, J.M., Pérez-García, J.M., Morales-Reyes, Z., Botella, F., Olea, P.P., Mateo-Tomás, P., Moleón, M., Hiraldo, F., Arrondo, E., Donázar, J.A., Cortés-Avizanda, A., Selva, N., Lambertucci, S.A., Bhattacharjee, A., Brewer, A., Anadón, J.D., Abernethy, E., Rhodes, O.E., Turner, K., Beasley, J.C., DeVault, T.L., Ordiz, A., Wikenros, C., Zimmermann, B., Wabakken, P., Wilmers, C.C., Smith, J.A., Kendall, C.J., Ogada, D., Buechley, E.R., Frehner, E., Allen, M.L., Wittmer, H.U., Butler, J.R.A., du Toit, J.T., Read, J., Wilson, D., Jerina, K., Krofel, M., Kostecke, R., Inger, R., Samson, A., Naves-Alegre, L., Sánchez-Zapata, J.A., 2019. Scavenging in the Anthropocene: Human impact drives vertebrate scavenger species richness at a global scale. Global Change Biology 3005–3017. https://doi.org/10.1111/gcb.14708

Sebastián-González, E., Moleon, M., Gibert, J., Botella, F., Mateo-Tomas, P., Olea, P., Guimaraes, P., Sanchez-Zapata, J., 2016. Nested species-rich networks of scavenging vertebrates support high levels of interspecific competition. Ecology 97, 95–105. https://doi.org/10.1890/15-0212.1

Selva, N., Jędrzejewska, B., Jedrzejewski, W., Wajrak, A., 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. Canadian Journal of Zoology 83, 1590–1601. https://doi.org/10.1139/z05-158

Smith, J.B., Laatsch, L.J., Beasley, J.C., 2017. Spatial complexity of carcass location influences vertebrate scavenger efficiency and species composition. Sci Rep 7, 10250. https://doi.org/10.1038/s41598-017-10046-1

Snowy Hydro Limited, n.d. The Snowy Scheme [WWW Document]. Snowy Hydro. URL https://www.snowyhydro.com.au/generation/the-snowy-scheme/ (accessed 8.15.21).

Snowy Monaro Regional Council, 2018. Snowy Monaro Regional Economic Development Strategy 2022 - Supporting Analysis.

Snowy Valleys Council, 2018. 2018 – 2022 Snowy Valleys Regional Economic Development Strategy 22.

Spencer, E., Newsome, T., 2021. Dingoes dining with death. Australian Zoologist 41, 433–451. https://doi.org/10.7882/AZ.2021.008

Spencer, E.E., Barton, P.S., Ripple, W.J., Newsome, T.M., 2020. Invasive European wasps alter scavenging dynamics around carrion. Food Webs 24, e00144. https://doi.org/10.1016/j.fooweb.2020.e00144

Spencer, E.E., Dickman, C.R., Greenville, A., Crowther, M.S., Kutt, A., Newsome, T.M., 2021. Carcasses attract invasive species and increase artificial nest predation in a desert environment. Global Ecology and Conservation 27, e01588. https://doi.org/10.1016/j.gecco.2021.e01588

Steffen, W.L., Natural Resource Management Ministerial Council (Australia), Biodiversity and Climate Change Expert Advisory Group (Australia), 2009. Australia's biodiversity and climate change: a strategic assessment of the vulnerability of Australia's biodiversity to climate change. Dept. of Climate Change, Canberra.

Strom, M., 2016. Kosciuszko explained: mystery of the Snowy Mountains solved [WWW Document]. The Sydney Morning Herald. URL https://www.smh.com.au/environment/kosciuszko-explained-mystery-of-the-snowy-mountains-solved-20160315-gnj2zg.html (accessed 9.14.21).

Sugiura, S., Tanaka, R., Taki, H., Kanzaki, N., 2013. Differential responses of scavenging arthropods and vertebrates to forest loss maintain ecosystem function in a heterogeneous landscape. Biological Conservation 159, 206–213. https://doi.org/10.1016/j.biocon.2012.11.003

Therneau, T.M., Grambsch, P.M., 2000. Modeling survival data : extending the Cox model, Statistics for biology and health. Springer, New York.

Tourism Research Australia, 2020. Regional Tourism Satellite Account 2019–20 | Tourism Research Australia [WWW Document]. Tourism Research Australia. URL https://www.tra.gov.au/data-and-research/reports/regional-tourism-satellite-account-2019-20/regional-tourism-satellite-account-2019-20 (accessed 8.15.21).

Turner, K., Abernethy, E., Conner, L., Olin, E., Beasley, J., 2017. Abiotic and biotic factors modulate carrion fate and vertebrate scavenging communities. Ecology 98, 2413–2424. https://doi.org/10.1002/ecy.1930

Turner, K.L., Conner, L.M., Beasley, J.C., 2020. Effect of mammalian mesopredator exclusion on vertebrate scavenging communities. Sci Rep 10, 2644. https://doi.org/10.1038/s41598-020-59560-9

United Nations Educational, Scientific and Cultural Organization, 2015. Kosciuszko | United Nations Educational, Scientific and Cultural Organization [WWW Document]. Ecological Sciences for Sustainable Development. URL http://www.unesco.org/new/en/natural-sciences/environment/ecological-sciences/biosphere-reserves/asia-and-the-pacific/australia/kosciuszko/ (accessed 5.27.21).

van der Plas, F., 2019. Biodiversity and ecosystem functioning in naturally assembled communities. Biological Reviews 94, 1220–1245. https://doi.org/10.1111/brv.12499

van Eeden, L.M., Smith, B.P., Crowther, M.S., Dickman, C.R., Newsome, T.M., 2019. 'The dingo menace': an historic survey on graziers' management of an Australian carnivore. Pac. Conserv. Biol. 25, 245. https://doi.org/10.1071/PC18031

Vass, A., Barshick, S., Sega, G., Caton, J., Skeen, J., Love, J., Synstelien, J., 2002. Decomposition Chemistry of Human Remains: A New Methodology for Determining the Postmortem Interval. J. Forensic Sci. 47. https://doi.org/10.1520/JFS15294J

Vicente, J., VerCauteren, K., 2019. The Role of Scavenging in Disease Dynamics, in: Olea, P.P., Mateo-Tomás, P., Sánchez-Zapata, J.A. (Eds.), Carrion Ecology and Management, Wildlife Research Monographs. Springer International Publishing, Cham, pp. 161–182. https://doi.org/10.1007/978-3-030-16501-7_7

Ward-Jones, J., Pulsford, I., Thackway, R., Bishwokarma, D., Freudenberger, D., 2019. Impacts of feral horses and deer on an endangered woodland of Kosciuszko National Park. Ecological Management & Restoration 20, 37–46. https://doi.org/10.1111/emr.12353

Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M., Getz, W.M., 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. Journal of Animal Ecology 72, 909–916. https://doi.org/10.1046/j.1365-2656.2003.00766.x

Wilmers, C.C., Getz, W.M., 2004. Simulating the effects of wolf-elk population dynamics on resource flow to scavengers. Ecological Modelling 177, 193–208. https://doi.org/10.1016/j.ecolmodel.2004.02.007

Wilmers, C.C., Post, E., 2006. Predicting the influence of wolf-provided carrion on scavenger community dynamics under climate change scenarios. Global Change Biology 12, 403–409. https://doi.org/10.1111/j.1365-2486.2005.01094.x

Wilson, E.E., Wolkovich, E.M., 2011. Scavenging: How carnivores and carrion structure communities. Trends in Ecology and Evolution 26, 129–135. https://doi.org/10.1016/j.tree.2010.12.011

Wimbush, D.J., Costin, A.B., 1983. Trends in drainage characteristics in the subalpine zone at Kosciusko.

Woinarski, J.C.Z., Braby, M.F., Burbidge, A.A., Coates, D., Garnett, S.T., Fensham, R.J., Legge, S.M., McKenzie, N.L., Silcock, J.L., Murphy, B.P., 2019. Reading the black book: The number, timing, distribution and causes of listed extinctions in Australia. Biological Conservation 239, 108261. https://doi.org/10.1016/j.biocon.2019.108261

Wyborn, C., 2009. Managing change or changing management: climate change and human use in Kosciuszko National Park. Australasian Journal of Environmental Management 16, 208–217. https://doi.org/10.1080/14486563.2009.9725236

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